Systematic Zoology

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Notes on Nomenclature

Decisions, Cooperative or Personal?	*J. C. Bradley*	101
Whither Zoological Nomenclature?	*W. A. Gosline*	107
Inadvisability of New Names in Abstracts	*J. L. Laffoon*	109
Cephalocarida and Crustacean Phylogeny	*H. L. Sanders*	112
History of Avian Classification	*B. G. Beddall*	129
Evolutionary Lines in Water Mites	*R. Mitchell*	137
People and Projects		149

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Systematic Zoology

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Nomenclature

In anticipation of the forthcoming Colloquium on Zoological Nomenclature, to be held in connection with the XVth International Congress of Zoology (see notice in "People and Projects"), it seems appropriate to consider the status, aims, and problems of our efforts to regulate zoological nomenclature. It is hoped that the three papers printed below—by BRADLEY, GOSLINE, *and* LAFFOON—*can be followed in subsequent issues by others similarly concerned with the broad aspects and implications of nomenclatural regulation.*

Cooperative or Personal Decisions on Zoological Nomenclature?

J. CHESTER BRADLEY

A DISTINGUISHED entomologist has recently discussed the name that should properly be applied to the family known in the vernacular as spider-hunting wasps. While I dislike entering into polemics, especially with a former student and warm personal friend whose taxonomic (if not nomenclatural) work I hold in high esteem, silence could be construed as tacit approval and acceptance of views that I feel obliged to repudiate. Also, this seems a good opportunity to comment on fundamentally different attitudes toward the treatment of zoological nomenclature. In order to keep my criticism impersonal I shall refrain from mentioning the name of the offender, but shall refer to him as "Dr. K." (which is not his initial).

Some of Dr. K's positive statements concerning the International Commission on Zoological Nomenclature and its motives are his opinions, backed by no citation of instance or fact. Some of my refutations will be simply my opinions. But, I may point out, I have had twenty-two years of close association with the Commission, involving ample opportunity to observe its motives. Dr K. has had none.

I shall quote successive sections from Dr. K's paper, letting my remarks follow each:

1. *"Pompilidae, rather than Psammocharidae is a name sometimes used for this family, but it may not be so used correctly."*

Wrong. *Only* Pompilidae can be used "correctly." Dr. K. means to say that under his personal code of zoological nomenclature Pompilidae can not be used correctly; or perhaps it would be better to say: Under the International Code, insofar as he personally sees fit to follow it. During the present century the International Code of Zoological Nomenclature has been the only general code recognized by zoologists and for that matter also by paleontologists. Under that code only Pompilidae is correct. That is true because one or more international congresses of zoology have directed the Commission to suspend the ordinary operation of one or more provisions of the code, if need be, and to establish a name or names in conformity with usage, where con-

fusion among names exists, or when continuity of long established usage is threatened, or diversity of usage has sprung up. This involves acting as arbiter in deciding what name shall be used in case two or more are in current use or dispute. Such action, when taken, is strictly under the provisions of the code, even in suspending conflicting provisions, and is just as legal as action under any other provision. Since such action has been taken for *Pompilus* and Pompilidae, these and only these are the correct terms to use.

2. *"The generic name* Pompilus *Fabricius 1898* [Dr. K. means 1798], *type of the family name Pompilidae, has* Pompilus viaticus *Fabricius as its genotype."* [1]

Wrong. The type of *Pompilus* is *P. pulcher* Fabricius, 1798, a spider-hunting wasp. When the Commission learned that a provision of the Code would fix *Pompilus viaticus* F. (a sphecid wasp) as type of Pompilus and would transfer that name (which with its family-name Pompilidae had been universally used for more than a century for spider-hunting wasps) to sphecid wasps,[2] they suspended that provision and fixed *P. pulcher* Fabricius as its type. Therefore, as shown in section (1) above, *pulcher* is the type-species under the code.

3. "Pompilus viaticus *is a species of Sphecidae, because of which the generic name* Pompilus *may be used correctly only in the Sphecidae."*

Would be true if it *were* the type-species of *Pompilus.*

4. *"In regard to the name Psammocharidae, its type genus is* Psammochares *Latreille, 1896* [Dr. K. means 1796], *with the genotype* Sphex fusca *Linnaeus.* Fusca *is a species of the subfamily Psammocharinae in the present family."*

Psammochares and Psammocharidae, having been suppressed by the Commission under empowering provisions of the Code, have no longer any status whatsoever as zoological names, *cf.* section 1.

5. *"The generic name* Psammochares *is the oldest name in the family and as such may be used as the type of the family name. . . ."*

Wrong. May I be pardoned for pointing out that this statement involves both some confused thinking and disregard of pertinent provisions of the International Code. No rule of any code provides that the oldest nominal genus within a taxonomic family must be its type-genus. *Psammochares* would not have become the type-genus of the family of spider-hunting wasps under the provisions of the International Code, even if none of them had been suspended. The "type-genus" of a family is a nominal genus, not a taxonomic genus. Therefore when it was discovered that the type-species of *Pompilus* was a thread-waisted wasp, the nominal genus *Pompilus,* type of Pompilidae, would have passed into the family of thread-waisted wasps. That would have left the taxonomic family of spider-hunting wasps either without a name, or with one to be uncovered from preceding literature. Some zoologists have assumed that, in such a case, the valid name of the taxonomic genus vacated by the name *Pompilus* would automatically become type of a new family name—*Psammochares* type-genus of Psammocharidae. That is a confusion of the issue, and not in accordance with the Code. The latter provides that "The naming of units belonging to the Family-Group of categories shall be governed by priority." (*cf.* Copenhagen Decisions on Zoological Nomenclature, 1953, p. 33, par. 45, 1). Therefore when the name Pompilidae, all along supposed to be correctly applied to the taxonomic family of spider-hunting

[1] An international congress of zoology has ruled that the term "type species" shall be used instead of "genotype" in the sense in which Dr. K. employs the latter word. The reason is that "genotype" has become firmly fixed in genetical literature with an entirely different meaning.

[2] Had this happened, the family names Pompilidae and Sphecidae, both attributed to Leach in 1815, would compete with each other for becoming the proper name of the family of thread-waisted wasps.

wasps, was removed to another taxonomic family, barring plenary suspension of the Rules, it would have left the spider-hunting wasps without any family name *unless some nominal genus within that taxonomic family had already become the type-genus of any category of taxa within the Family-Group.* If that had happened, the genus first so selected would have become automatically type of the family. This is a point into which Dr. K. has made no enquiry. If he had he would have learned that the genus *Aporus* had been selected as type of "Aporida" by Leach in 1815.[3] Not only Aporidae, 1815, and Ceropalidae but also all of the subfamily and tribal names used by Ashmead, 1900–1903, have priority over Psammocharidae and some one of these names, probably Aporidae, would have had to be adopted if the International Commission had not used its Plenary Power and conserved Pompilidae. Thus a newly confused situation would have arisen, with two family names in use each of which would have had to yield to a third one that no one now uses.

6. *"Older authors have used the name Pompilidae for the family without considering its validity, but in 1910 Banks introduced usage of the correct name, Psammocharidae, which steadily gained favor."*

"Psammocharidae" gained usage because several authors accepted Banks' statement that it was the correct name under the Code. That it gained *favor* by any one except Mr. Banks is highly questionable. Mr. Banks did not, and Dr. K. does not point out that Fox had previously attempted to change the name of the family to "Ceropalidae," and that this name, although still not then the correct name, had priority over Psammocharidae.

7. *"Psammocharidae . . . steadily gained favor until by a generation later the majority of the basic literature of the world used this name."*

By 1928, eighteen years after Banks attempted to change the name of the family to "Psammocharidae," seven specialists in the superfamily to which spider-hunting wasps belong were currently using *Pompilus,* while six were using *Psammochares.* Of 52 Hymenopterists who responded at that time to a questionnaire asking which name they were currently using, thirty-six said they were using *Pompilus,* only sixteen *Psammochares.* Ten of the latter were Americans, who, at that time, were more prone than other taxonomists to adopt such changes.

8. *"Certain workers who wished to continue using the name Pompilidae, however, appealed to the International Commission on Zoological Nomenclature."*

"Certain workers" gives a false impression. The action referred to occurred in 1928. At that time the view of every publishing hymenopterist in the world whose address could be ascertained was sought. Practically all replied and 59 of them (nearly all who did reply) asked to have their names joined to a petition that requested the Commission to reject the name *Psammochares,* and to validate *Pompilus* for the spider-hunting wasps. Two of the three chief specialists in the family at that time, Arnold and Haupt, joined the petitioners. The third, Banks, refrained because it was he who had proposed to resuscitate *Psammochares* and he felt that it would damage his prestige to reverse his position.[4]

9. *"Certain workers . . . appealed to the International Commission on Zoological Nomenclature for an arbitrary declaration that Psammocharidae was incorrect and Pompilidae was correct."*

[3] Edinburgh Encycl., v. 9, p. 189, according to Ashmead. I have not verified this reference, nor have I noted whether Leach established other Family-Group names among the spider-hunting wasps. However, Radoskovsky in 1888, or shortly thereafter, established the family-name Ceropalidae, Fox in 1901 used this as the correct name of all the spider-hunting wasps, and Ashmead about the same time acknowledged it as correct.

[4] This was apparent from an explanation given to me personally by Mr. Banks on a subsequent occasion.

"Arbitrary declaration" is scarcely the way to describe the discharge of a duty laid upon the Commission by the Monaco International Congress of Zoology, and requested by an overwhelming majority of the specialists in Hymenoptera in the whole world. The Commission was not asked to arbitrarily declare anything, nor did it do so. It used its authorized Plenary Powers to suppress the name *Psammochares* for nomenclatural purposes, to validate *Pompilus*, and to designate *Pompilus pulcher* F. to be the type-species of *Pompilus*.

10. *"The International Commission obliged by issuing in 1945 its Opinion No. 166."*

"Obliged" insinuates motives that are wholly false, and that should have really been beneath Dr. K. to imply. "Obliged" means "to bind by some favor or kindness rendered." It is inconceivable to me that personal favor has ever entered into the mind of any Commissioner in casting his vote on any question. It is outrageous to imply that there could have existed collective collusion to grant a favor in any instance. While Commissioners must rely upon the facts presented to them (carefully checked by the secretariat) and the advice and judgement of specialists, I doubt that there is ever a vote cast that does not represent the sincere judgement of the Commissioner who casts it as to what is best for zoology. What *is* best for zoology, he must conceive broadly, and not merely from the point-of-view of a specializing taxonomist.

However, the matter was not decided by the issuing of Opinion 166 in 1945, as indicated by Dr. K. It was practically decided and published some ten years earlier; though final decision did not come until 1939. When the Commission received the petition it asked the International Committee on Entomological Nomenclature for advice. This Committee recommended to the International Commission on Zoological Nomenclature that it "should use its plenary powers to preserve the long-established name *Pompilus* Fabricius, 1798, [with *P. pulcher* as type] with the family name Pompilidae, since, having regard to the literature as a whole, confusion rather than uniformity would result from the supercession of these names by the names *Psammochares* Latreille, 1796, and Psammocharidae."[5] This recommendation was confirmed by the Sixth Congress of Entomology on September 12th, 1935. Four days later the foregoing recommendation was adopted by the Commission on Zoological Nomenclature and on September 21, 1935, it was unanimously approved by the Twelfth International Congress of Zoology. However, there was one reservation attached: Owing to the illness of the retiring Secretary, the public had not been given the required full six months notice that the case was to be considered, therefore the new Secretary was directed to publish such notice and to hold the case open for six months thereafter. This was done, and since no Commissioner subsequently desired to change his vote the decision was made final on June 19, 1939, the delay being due to the difficulties arising from removing the secretariat from Washington to London. Publication of Opinion 166, embodying the decision, was delayed by reason of the Second World War until 1945. (These facts were all known to Dr. K., but ignored.)

11. *"Throwing its influence behind the usage of the name Pompilidae and against the name Psammocharidae"*

"Throwing its influence" implies that the matter was left open. It was not, it was definitely and permanently decided

[5] Neither the Entomological Committee nor the Zoological Commission examined the question as to whether Psammocharidae, as opposed to Ceropalidae or some other term, would have replaced Pompilidae if *Pompilus* and Pompilidae were not conserved in their customary sense. The petition did not raise that question, but incorrectly implied that it would be Psammocharidae. Whatever the name, it would have been an innovation; what name would have been correct was of no particular interest to the Commission.

by a body representing the zoologists of the world, empowered and directed to act.

12. *"This is one of a series of similar actions by the International Commission whose purpose has been to promote uniformity in zoological nomenclature and to gain additional support for itself by appeasing those zoologists wishing arbitrarily to maintain certain names."*

"Purpose has been . . . to gain additional support for itself by appeasing those zoologists" is such a grave charge as to suggest utter irresponsibility and intemperate behavior on the part of its author. It is amazing that any sane zoologist would lay such a charge without presentation of evidence or citation of instances, against an international body of eminent zoologists. He must certainly hold his profession in great contempt!

13. *"Wishing arbitrarily to maintain certain names in which their convenience and prestige were involved."*

Hardly worthy of reply. I do not suppose that "the convenience and prestige" of a petitioner has ever been taken into consideration by any Commissioner in casting a vote. If a petitioner can not convince some twenty-two minds, specialists in diverse fields, that what he asks is in the best interest not only of the field in which he specializes, but of zoologists as a whole, he will not get a favorable decision.

14. *"Rather than to submit the disposition of the names to impartial rules of procedure."*

Dr. K. implies, but supports the implication only with intemperate expressions of opinion, that the disposition of the names is not being submitted to "impartial rules of procedure."

15. *"Although a purpose of the International Commission was to decrease confusion, it has so often been misinformed on the specific cases and on certain general nomenclatorial situations that confusion has instead been multiplied."*

Another general charge, substantiated by no evidence or citation of instances. It is undoubtedly true that in the early days the Commission sometimes was given insufficient or inaccurate data which could not be rectified or completed because of a busy Secretary and no funds to employ help. The present administration makes every effort to verify facts presented to the Commission. The best advice of specialists on each case is sought. Every proposal is published in the *Bulletin of Zoological Nomenclature,* and the comments of all interested zoologists within a six-months period are not only invited, but carefully weighed by the Commissioners before votes are cast.

16. *"It is hard to see how the influence of these kinds of actions can endure indefinitely, and since their influence is considered temporary, they are disregarded and the name Psammocharidae is here retained."*

I assume that Dr. K. means that it is he who considers them temporary and disregards them. Or does he? His statement is so worded as to apply to the world at large.

One wonders, now that "Aporidae," or some other name, has been shown to be correct under the International Code, if it were shorn of the provisions giving the Commission its plenary powers, whether Dr. K. will adopt that name, or whether he will continue to "retain Psammocharidae," thus himself "succumbing to the influences of laziness and prejudice."

17. *"The human researcher never entirely escapes the influences of laziness and prejudice, but having striven at much cost for accurate and honest work* [*cf.* parenthetical statement at the end of section 10] *in the body of this paper, it would be inconsistent to abandon this course by adopting the family name Pompilidae. Such considerations, however, do not have an equal appeal to all workers, and many are now using the name Pompilidae on the authority of the International Commission on Zoological Nomenclature."*

In this final blast Dr. K. is, in effect, accusing even his fellow specialists in the spider-hunting wasps of having abandoned "accurate and honest work" and of having succumbed to "the influences of laziness and prejudice." This includes such men as Dr. Arnold, Dr. Evans, Dr. Hurd, and Dr. Priesner, not to mention this reviewer, all of whom have adopted "Pompilidae."

When the questionnaire looking toward petitioning the International Commission on the case of *Pompilus* was circulated to hymenopterists, each was asked which name he would use in the future, *Pompilus* or *Psammochares,* in case the Commission refused to validate *Pompilus.* Of the thirty-two who replied to this question, seventeen, one more than a majority, said that they would continue to use Pompilus in any event. Seven of these thirty-two were specialists in the superfamily to which the spider-hunting wasps belong, and four of these seven said that they would continue to use *Pompilus* anyway. No better proof could be adduced of the futility of trying to force zoologists to follow highly technical rules when their observance would demand the abandoning of long-established, universally used, important zoological names.

The sessions of the Paris meeting of the International Commission on Zoological Nomenclature in 1948 were open to all interested zoologists, and were well attended. World-wide sentiment was apparent that when general usage of a name has become established, no technical rule should be allowed to overthrow it. In 1953 fifty-one zoologists were gathered in the Colloquium on Nomenclature at Copenhagen and the same world-wide sentiment was not only paramount but was translated into action that, in effect, preserves all names which have incontestably been in general use in a particular sense over a long period.

This sort of thing is common sense, because zoological names are part of language, and like all language become fixed by custom. No nomenclatural rule involves absolute right or wrong. No question of scientific accuracy is involved, merely one of the greater public convenience. The rules do not exist to glorify the founders of names; their sole purpose is to prevent chaos by establishing uniformity and continuity of usage throughout the world, and zoologists, in the long run, will not tolerate any interference with this aim. The voices of those erudite taxonomists who stand for the letter of the law at whatsoever inconvenience to their colleagues are becoming increasingly more feeble, now that an effective representative body exists that can make decisions in favor of continuity in the name of the united body of world zoologists. The aim of these taxonomists is as impossible of achievement, as would be an attempt of philologists to restore the original form and meaning of all words. Is it preferable, from any point-of-view, to struggle along through the centuries in the name of obeying the law, from Pompilidae to Ceropalidae, to Psammocharidae to Aporidae and one knows not what other name in the future, disrupting the literature of each period from that of every other period, than it is to have a clear-cut decision by a central authorized body that will tie up the literature of the preceding two centuries with that of the future to the maximum extent that is possible?

So I come to the question that gives title to this essay: Is it better to depend upon personal interpretations of a nomenclatural code that is devoid of provisions for relief, letting the chips fall where they may, or to obtain the maximum degree possible of continuity and universality in literature and practise, by the world-wide cooperation of zoologists in setting up a central commission dedicated to that end?

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Whither Zoological Nomenclature?

WILLIAM A. GOSLINE

ZOOLOGICAL nomenclature appears to be approaching a fork in the road. At first sight nomenclatural thinking might appear to be travelling two, perhaps three, different roads at once, but a sounder interpretation is probably that it is in the throes of contemplating a change in direction. In any event the phenomenon affects all zoologists and consequently deserves their careful consideration. The present discussion of these apparent lines of nomenclatural thought is not only preliminary but it is written by one who is interested in nomenclature only in so far as it provides a useful tool for zoological work.

The 1901 edition of the Rules of Zoological Nomenclature was based on the principle that if one followed certain prescribed procedures one would arrive at (or if necessary create) the valid scientific name of an animal, and that if everybody would follow the same path he would arrive at the same name. The utility of this concept is directly correlated with the simplicity of the procedures. If these become so complicated that only a nomenclatural technician can determine the valid name, then the amateur, i.e., the zoologist, will go astray. Under such circumstances the recognition value of the valid name would be greatly reduced and the amount of time necessarily transferred from zoological to nomenclatural work increased; in short the value of nomenclature as a zoological tool would be greatly impaired. There is, however, another and more dire possibility, namely that zoologists would simply ignore the Rules, using whatever names they saw fit. If this happened, zoology would revert to the dark nomenclatural ages before there were any Rules. (Unfortunately or fortunately, the International Commission has no enforcement agency other than zoological opinion. This point seems sometimes to have slipped from sight.)

Two nomenclatural concepts that can or do lead off in rather different directions have now been superimposed on the procedural method dealt with above. The first of these has its origin in the Opinions. The earlier Opinions took up either applications of the Rules to moot cases or amplifications of the Rules to cover deficiencies. With time, however, the Opinions became increasingly diverted to *ad hoc* decisions concerning the validity of individual scientific names, e.g., nos. 67, 73, etc. From there it was but a short and logical step to the establishment of the present list of *nomina conservanda*. Suffice it to say for the moment that any name placed on this list becomes *ipso facto* the valid name regardless of the Rules. The second innovation is the recent concerted effort to insert into the Rules some law ensuring the conservation of well-known scientific names. The exact framing of such a concept does not seem to have been worked out, but the intent is to prevent the changing of well established names, again regardless of the Rules. These then are the two concepts that seem to point in a somewhat different direction from the old Rules, and it seems advisable to pause and consider where the various roads of nomenclatural thought lead.

The Rules themselves have followed a path toward increasing complication. To point up the resulting difficulties, a personal example with obvious defects will here be risked. In teaching nomenclature in a course on systematic zoology over a number of years the author has found it best to start with the 1901 Rules. Stu-

dents can and do grasp these, and it is fondly assumed that they will pick up the subsequent minor modifications at need; in any event the students are off on the right track. On the other hand, attempts to start with the more recent expositions of the Rules have generally resulted in the students' failure to distinguish the main outlines of the forest because of the trees and shrubs. On the basis of this limited experience the author has often hoped that the really major points in the forthcoming edition of the Rules would be printed in large type and simple language, with the minor restrictions, amplifications, etc., confined to footnotes in small type. If, however, the new Rules form a long, involved document, then for the good of zoology it might be well if somebody would rephrase them in such a way that the main points will be readily distinguishable and assimilable. Unfortunately the announced intent to copyright the new Rules would seem to put a stop to any such effort. (The author has always considered the Rules as public property. To have the copyright appropriated by the International Trust seems to him at best unethical; at worst it could provide zoologists with an excuse for ignoring the Rules completely.)

As compared with the 1901 procedural approach, the *nomina conservanda* principle could lead in a very different direction. Followed to its conclusion, the list would include all valid zoological names. If this happened one could ignore the Rules and simply look up the valid name in a book that would doubtless resemble a nomenclator. It would, of course, be many years before such a book could be compiled, and the difficulties of compilation are at present unassessable.

Any law of conservation (or usage) could open a road in still a different direction. If followed out, this could end with zoologists again ignoring the Rules but rather establishing validity by determining which of two or more names for an entity had been most frequently used. One trouble here, of course, is in defining usage. Certainly no strict criteria are possible or they would have been settled on long ago. Nevertheless, it seems that even with inexact criteria the International Commission could be left to decide the many disputable cases that would certainly arise. In this respect the principles of usage and of *nomina conservanda* might be made to dovetail with one another.

As viewed by this author, then, the present status of zoological nomenclature is somewhat as follows. The system of Rules has been becoming increasingly complex and unwieldy. Two methods of cutting across the Rules have developed: the *nomina conservanda* and the principle of usage. Both of these methods hold the potentiality of shortcircuiting the Rules and of sending zoological nomenclature off in a new and uncharted direction. Whether nomenclature will set out in such a new direction at the expense of the old system of Rules, or whether some harmonious compromise can be worked out between apparently incompatible lines of thinking remains to be seen.

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On the Inadvisability of Including New Nomenclatural Information in Abstracts

JEAN L. LAFFOON

DISSERTATION ABSTRACTS, formerly known as *Microfilm Abstracts,* is a serial publication of University Microfilms, Ann Arbor, Michigan. Sixteen volumes of this serial had appeared by the end of 1956. University Microfilms has a cooperative agreement with over seventy academic institutions whereby abstracts of doctoral dissertations accepted at these institutions are published in *Dissertation Abstracts.* Microfilms of any of these dissertations may be purchased by interested individuals.

Abstracts in *Dissertation Abstracts* are to be considered duly published for nomenclatural purposes since they meet the requirements for publication set forth in Conclusion 15 of the VIIth (Paris) meeting of the International Commission on Zoological Nomenclature (1950) in 1948. In Conclusion 16 of the same meeting the Commission agreed to "recommend" that new names not be published in abstracts issued in advance of the published work containing the descriptions of the taxonomic units. The Copenhagen Decisions on Zoological Nomenclature (1953) include a decision (pp. 60-61) that new names in papers distributed on microfilms are not to be considered as published.

Numerous new names, new combinations, and other taxonomic changes for animal names are being published in *Dissertation Abstracts.* The examples given below are taken from the Zoology section of the 1955 and 1956 volumes of the serial.

Actions in accordance with the Rules. Stough (1955) gave a description of a new genus and species of parasitic nematode which probably is adequate under the Rules. Wurtz (1955) transferred two subfamilies of snails to the status of family Hadley (1955), in an abstract on bat taxonomy, revived a genus, reduced two genera to the status of subgenus, indicated new synonymy, and made several new combinations. Savage (1955) created a new subfamily name for lizards. Crenshaw (1955) removed the species name of a turtle from synonymy and made a new subspecific combination for another turtle name. Kormondy (1955) indicated new synonymy for some dragonfly names. Adams (1956) created four new tribes for birds (at least one of the tribes will date nomenclatorially from some earlier paper, as it is based on the type genus for the family). He also gave a case of new generic synonymy and three new combinations of specific and subspecific names. Moore (1956) transferred two Homoptera to different subfamilies and sank three specific names as junior synonyms. Levin (1956) showed a case of new specific synonymy in nematodes. Gibbs (1956) sank a generic name of a fish as a junior synonym. Johnson (1956) revived a combination in nematodes. Auffenberg (1957) gave new generic and specific synonymy for snakes.

Actions not meeting requirements of the Rules. Caine (1955) created a nude subspecific name and a nude specific name for protozoans. Savage (1955) erected a nude generic name for lizards. Namba (1955) coined thirteen nude spe-

cific names for flies. Sleeper (1956) created three nude generic and five nude specific names for weevils. Auffenberg (1957) formed four nude generic names and two nude specific names for snakes.

Probably the authors who included new nomenclatural information in their abstracts should not be criticized. Some of them may not have been sufficiently familiar with the Rules to realize what they were doing—certainly familiarity with the Rules is not easily attained at present. Some may have submitted abstracts to their institutions without knowing that the abstracts were to be published. And there may be other extenuating circumstances.

Although the abstracts referred to in this paper were all published in *Dissertation Abstracts*, it may be noted that certain universities publish similar abstracts of dissertations. Some such abstracts contain nomenclatural information comparable to that in the abstracts cited here.

All taxonomists know cases in which publication of a nude name has led to a long history of grief and confusion regarding the valid name for a species and the dates to be used for priority purposes. Likewise the publication of taxonomic work in "preprints" prior to general release (a situation partially paralleling the present case) has given rise to difficulties. Most taxonomists probably agree that publication of new names, new combinations and the like in abstracts without adequate description and/or comments is poor taxonomic practice. The International Commission (1950) has already recommended against the practice of publishing new names in abstracts. Clearly, action is needed to stop this flow of nude names and of changes in status of names accompanied by little or no discussion. Several plans of action might be followed, including:

(1) *Ignore names, etc. published in abstracts.* Probably some taxonomists will ignore all names and changes published in abstracts whether or not they meet the requirements of the rules. Others will probably bring the names into use, including some which are not in accordance with the rules. With some workers ignoring and some recognizing work published in abstracts, confusion is inevitable.

(2) *Appeal to the Commission to declare that publication in an abstract does not constitute publication for nomenclatural purposes.* Such action by the Commission would settle the issue, but it might take years to get the Commission to act. The names and notices of changes would still receive wide distribution and could still lead to confusion.

(3) *Cessation of publication of taxonomic abstracts.* This would eliminate the problem, but would require the agreement of each of the institutions involved and thus probably is not feasible.

(4) *Delay in publication of the taxonomic abstracts.* If the dissertations were published in their complete or modified form before the abstracts appeared, the nomenclatural information in the abstracts would be outdated by the published papers. But this would involve the loss of much of whatever advantage there is in publication of the abstracts. And many dissertations are never published, or only limited sections finally appear in print. This scheme would also require the cooperation of the individual schools and probably is not feasible.

(5) *Deletion from the abstracts of all new names and changes of status of names.* If each taxonomy student and each professor directing taxonomic studies would cooperate in this plan, the nomenclatural problems created by the abstracts could be eliminated. Examination of recent taxonomic abstracts shows that some authors (probably on advice of their professors) are not mentioning by name the new taxa in their papers, but simply state the number of new species, etc. involved. However, some have avoided giving the names but have included new synonymy or transferred old names to a new status.

Of the five plans mentioned, I recommend that Plan 5 be given a trial. It has

the advantage of requiring only that individual taxonomists see that changes of status of names and new names are not included in abstracts that they or their students submit. If after a period of two or three years it is apparent that many abstracts are still objectionable on nomenclatural grounds, perhaps taxonomists should resort to Plan 2.

Following is a statement approved by the Iowa State College Graduate Faculty for inclusion in its manual on thesis preparation; other institutions might well consider adopting a similar statement:

> Authors preparing theses in taxonomy are strongly urged to work closely with their major professors in the preparation of abstracts in order to avoid the premature publication of previously unpublished names of organisms, synonyms, new combinations, and nomenclatural changes. New scientific names, or taxonomic changes affecting bacteria, plant, and animal names appearing in *Dissertation Abstracts* are effectively published under international rules governing bacteria, plant, and animal nomenclature. These international codes of nomenclature strongly discourage the use of abstracts as a medium of publication.

REFERENCES

COPENHAGEN DECISIONS ON ZOOLOGICAL NOMENCLATURE. 1953. London, Printed by order of the International Trust for Zoological Nomenclature.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1950. Conclusions 15–16. (of the 7th Meeting held at Paris in 1948). *Bull. Zool. Nomencl.*, *4*:215–222.

All of the following are abstracts published in Dissertation Abstracts:

ADAMS, T. 1956. Comparative osteology and phylogeny of the family Ardeidae. *16*:1740.

AUFFENBERG, W. 1957. A study of the fossil snakes of Florida. *16*:2560.

CAINE, R. L. 1955. A morphologic and taxonomic study of the flagellated enteric protozoa of leeches. *15*:1465.

CRENSHAW, J. W. 1955. The ecological geography of the *Pseudemys floridana* complex in the southeastern United States. *15*:2349.

GIBBS, R. H., JR. 1956. A systematic study of the cyprinid fishes belonging to the subgenus *Cyprinella* of the genus *Notropis*. *16*: 409.

HADLEY, C. O. 1955. A revision of the American bats of the genera *Euderma* and *Plecotus*. *15*:1466.

JOHNSON, A. A. 1956. Life history studies on *Hydromermis contorta* (Kohn), a nematode parasite of *Chironomus plumosus* (L.). *16*: 409–410.

KORMONDY, E. J. 1955. Studies on the life history, morphology and ecology of the genus *Tetragoneuria* in Michigan (Odonata: Libellulidae). *15*:2353–2354.

LEVIN, N. L. 1956. Life history studies on *Porrocaecum ensicaudatum*, an avian nematode. *16*:1969.

MOORE, T. E. 1956. Evolution of the higher categories of Cercopidae, with a revision of the North American species of *Aphrophora* (Homoptera). *16*:1743–1744.

NAMBA, R. 1955. A revision of the genus *Rivellia* (Otitidae, Diptera) of North America north of Mexico and the external anatomy of *Revellia* (*sic!*) *winifredae* Namba. *15*:1934–1935.

SAVAGE, J. M. 1955. The lizard family Xantusiidae: an evolutionary study. *15*:1936–1937.

SLEEPER, E. L. 1956. The snout beetles of Ohio (Coleoptera, Curculionoidea) (Volumes I and II). *16*:2249–2250.

STOUGH, B. D. 1955. *Lynxrufus wilsoni* n.g., n.sp. (Nematoda: Metastrongylidae) from the lungs of the bobcat, *Lynx rufus rufus* (Shreber). *15*:175.

WURTZ, C. B. 1955. The American Camaenidae. *15*:906.

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The Cephalocarida and Crustacean Phylogeny

HOWARD L. SANDERS

CRUSTACEAN phylogeny has intrigued zoologists for almost one hundred years. Despite the long sustained interest, this problem still remains largely unclarified due to the fact that each subclass forms a sharp, clearly defined taxonomic unit.

Initial observations (Sanders, 1955) on the newly described crustacean *Hutchinsoniella macracantha* seemed to disclose affinities with the more primitive representatives of the subclasses Branchiopoda, Malacostraca and Copepoda. In an effort to indicate crustacean phylogeny as well as to illustrate the affinities of the Cephalocarida with the extant subclasses of Crustacea, this second paper will compare the Paleozoic arthropods, particularly the Crustacea, with the crustacean subclass Cephalocarida, as exemplified by *Hutchinsoniella*.

Subsequent to the original description, which was based on eight individuals, 320 additional specimens, representing all free-living stages of *Hutchinsoniella macracantha*, have been collected from Long Island Sound, and more recently, Buzzards Bay, Massachusetts by this investigator. On the basis of this material a few observations on the life history of *Hutchinsoniella* and some additional pertinent details on cephalocarid anatomy can now be discussed. These animals are found subtidally in soft mud where the benthic fauna is dominated by the polychaete *Nephthys incisa* and the lamellibranch *Nucula proxima*. A description of development from hatching to maturity will be presented in a subsequent paper.

Recent studies reveal that *Hutchinsoniella* is a hermaphrodite with entirely separate functional ovaries and testes (manuscript in preparation). Individuals are ovigerous from June through September and carry two ovisacs each attached by a short stalk to the limb rudiments of the genital segment. Each ovisac contains a single embryo. Observations in the laboratory indicate that a female can bear only three broods or six embryos during the breeding season. This is a remarkably small recruitment for a marine invertebrate.

Morphological Findings

Additional specimens have made it possible to describe more completely and to reinterpret cephalic and thoracic appendages (Figs. 1, 2 and 3) as well as to observe that ten rather than nine somites comprise the abdomen of the adult. Setae are missing on some of the limb figures and, unless otherwise stated, are considered as being lost in the preparation of the slide. Very fine hairs can be shown on setae and certain limb segments. It is assumed that these very fine structures may be present but not discernable on limbs, limb segments or setae that appear to lack them. The first thoracic appendage in the initial description is now considered to be the second maxilla. The reason for this interpretation is given on page 124, line 3. As a result, there are nine postcephalic appendages rather than ten, and twenty postcephalic segments, including the telson. A thoracic appendage, such as limb three, corresponds to limb four of the original description.

First antennae or antennules (Fig. 1, *A*): with six wide basal points and thin terminal strap-shaped filamentous portion of about 35 joints. Distal surface of second basal segment bearing small single-jointed flagellum with two setae (*B*). Initial joint of filament about equal to length of next four. Clusters of six and five setae on distal edges of third and sixth basal segments.

Second antennae (Fig. 1, *C*): with two-

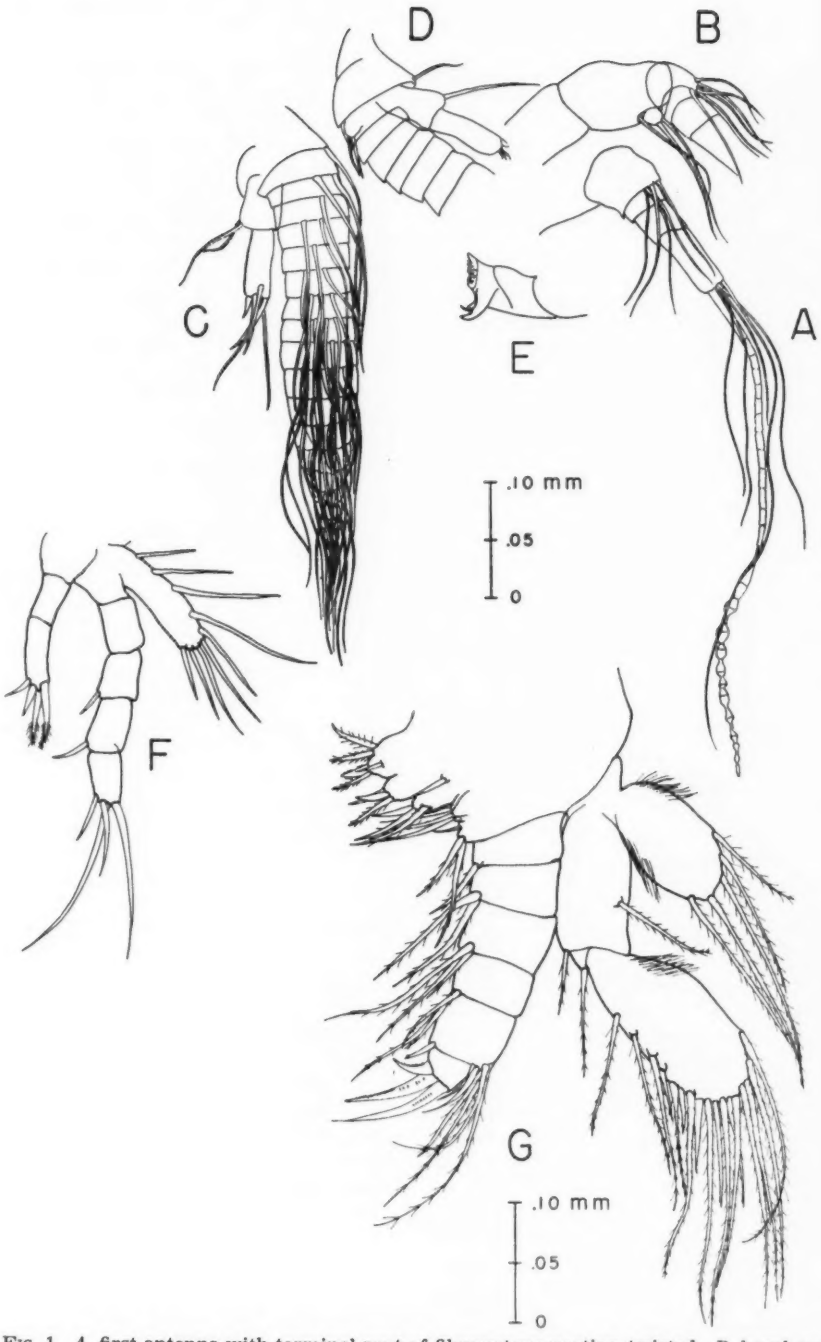

FIG. 1. *A*, first antenna with terminal part of filamentous portion twisted. *B*, basal section of first antenna, showing small articulating knob. *C*, second antenna. *D*, basal section of second antenna, showing knoblike eminence. *E*, mandible. *F*, first maxilla. *G*, second maxilla.

jointed protopodite, bearing knoblike eminence with setae (*D*), and two rami, one a two-jointed endopodite with second segment rectangular with two spines and three setae on distal end, other a large club-shaped exopodite composed of about eighteen joints covered with numerous long setae.

Mandibles (Fig. 1, *E*): without palp, median surface forming grinding molar plate covered with numerous tiny papillae and incisor component of two spines with movable bristle in between.

First pair of maxillae (Fig. 1, *F*): biramous protopodite with elongate two-jointed gnathobase bearing four spines on distal end, two of which have terminal portion covered with fine hairs; five-jointed endopodite with single spine on second and third segments with one long and two shorter spines on fourth segment and terminating with long spine-like dactyl; single-jointed flattened oblong exopodite with nine setae on lateral and distal margins.

Second maxillae and first eight thoracic limbs: all essentially similar. Thoracic appendages six, seven and eight (Fig. 3, *B*, *C* and *D*) successively smaller in size. Thoracic appendage nine has two segments, a small round distal joint on anterior part of larger oblong segment (Fig. 3, *E*). Protopodite apparently unsegmented although there are indications of a possible precoxal suture. Endopodite seven-jointed, distal segment dactyl with shorter medial and longer lateral spine inserting on penultimate segment about half as wide as more proximal joints; segments two, three, four and five similar; segment one wider than others with medial margin longer than lateral. Setae on outer distal edge of first five segments with one or two on first, two or three on second, two or three on third, three on fourth and one on fifth segment, usually haired; cluster of six setae on inner distal margin of fifth segment; terminal spines and dactyl with series of small teeth on inner surface. Endopodite of seventh appendage (Fig. 3, *C*) with fewer setae on each segment, one long spine with teeth rather than cluster of setae on inner margin of fifth segment; long terminal spine fused with dactyl to form elongate conical structure slightly globular at apex which with penultimate segment is markedly flexed toward the midline. Eighth limb with endopodite absent, Fig. 3, *D*). Exopodite four-jointed, flattened; ultimate joint circular in outline, about eighteen setae fringe distal and medial margin with longest on distal edge, setae of two kinds, approximately twelve or thirteen haired setae and four or five shorter bifid setae inserted in slightly different plane, numerous very fine hairs bordering proximal lateral margin; penultimate segment (fused to segment two in appendage eight) small and triangular on medial aspect of ramus and bearing single seta at apex; second segment hexangular, with single seta on distal medial edge, absent on eighth limb and single seta on lateral margin missing on limbs six, seven and eight; first segment somewhat triangular with outer edge giving rise to flattened oar-like pseudepipodite with about seven or eight haired setae on distal third of segment with perhaps less setae on limb eight, both proximal margins bordered by numerous fine hairs.

Medial surface of protopodite with complex six-lobed gnathobase, except five-lobed on second maxilla; gnathic processes reduced on appendage eight. All lobes articulate; proximal four lobes (three in second maxilla) larger; first with two hairy short setae on proximal edge and two short thick spines, one of which is toothed, on medial surface with single short seta inserting below and between spines; second lobe similar to first with two spines and single seta; third lobe with three spines and one seta; fourth with three spines and one or two setae; fifth and sixth lobes each with two setae; somewhat parallel row of about twelve or thirteen setae, oriented at slightly more oblique angle, present along base of lobes. Lines of very fine hairs on the protopodite and endopodite (Fig. 2, *C* and *D*) of some limbs, and combs of hair present on some appendages near proximal medial edge of protopodite (Fig. 2,*D* and Fig. 3,*C*).

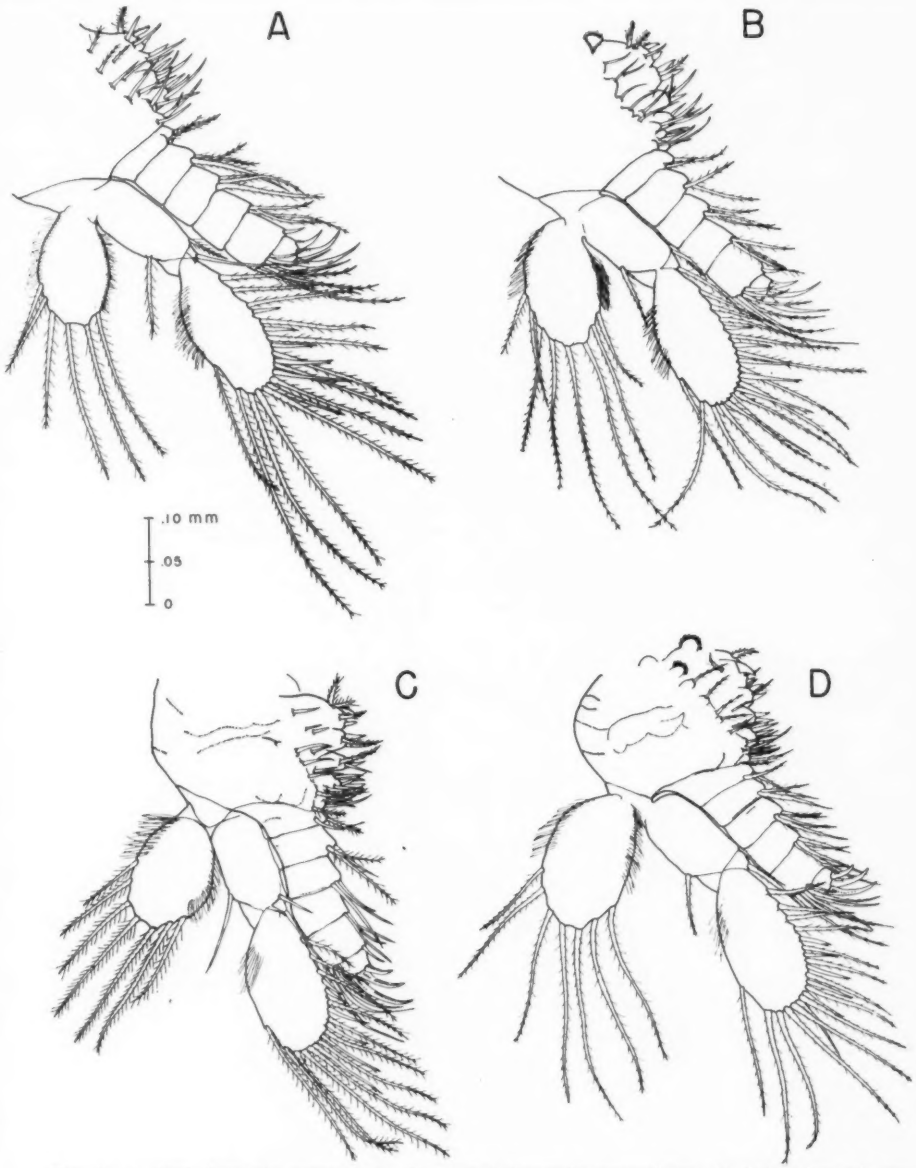

FIG. 2. *A*, first thoracic appendage. *B*, second thoracic appendage. *C*, third thoracic appendage. *D*, fourth thoracic appendage.

Paleozoic Arthropods

It has been assumed by many paleontologists and zoologists that the long extinct arthropods known as trilobites were the ancestors of the Crustacea. Except for the first pair of cephalic limbs which were uniramous, these primitive animals car-

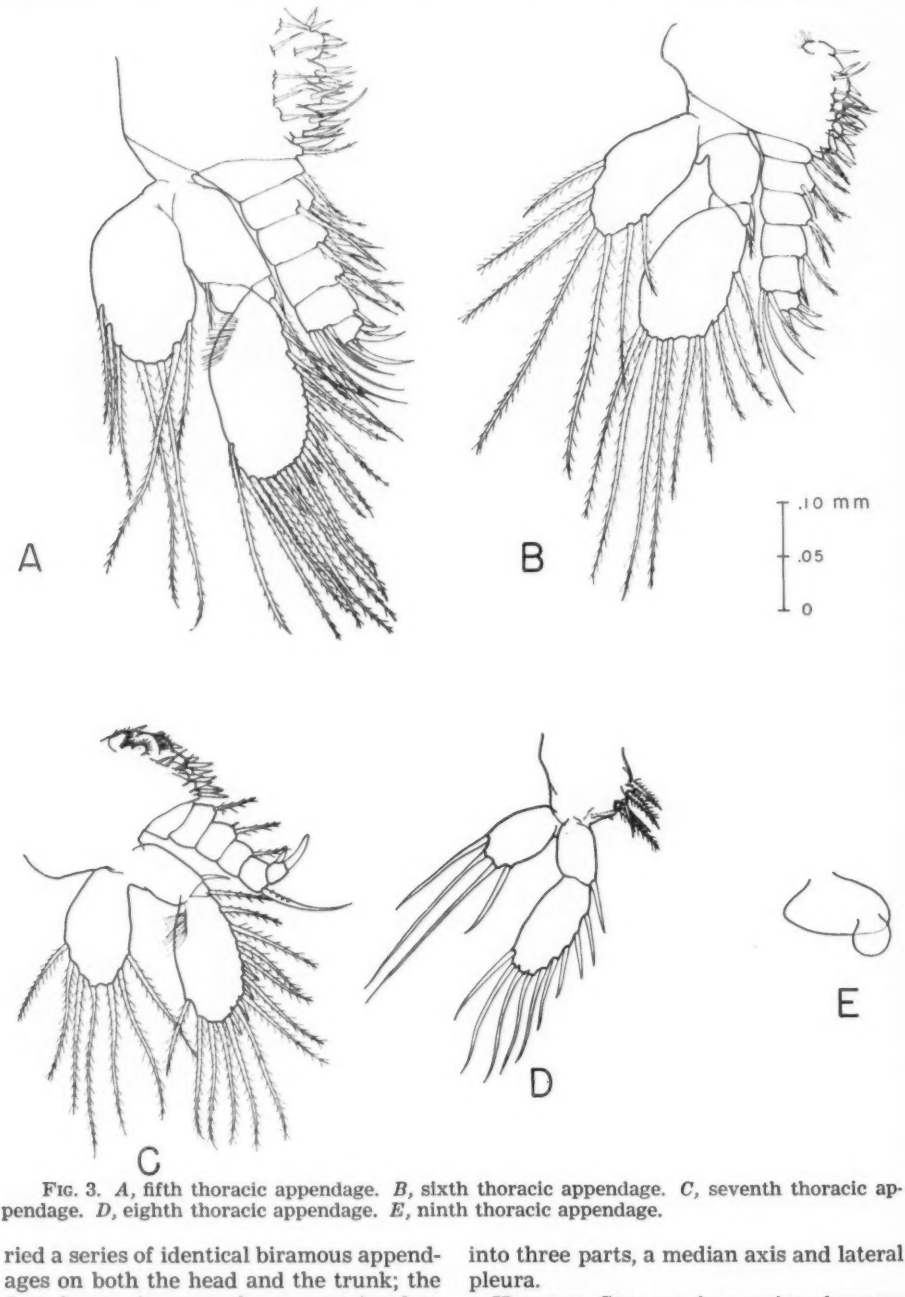

FIG. 3. *A*, fifth thoracic appendage. *B*, sixth thoracic appendage. *C*, seventh thoracic appendage. *D*, eighth thoracic appendage. *E*, ninth thoracic appendage.

ried a series of identical biramous appendages on both the head and the trunk; the first four pair were always restricted to the head. The dorsal shield was divided into three parts, a median axis and lateral pleura.

However, Størmer, in a series of papers (1939, 1942, 1944) dealing with trilobite

morphology took sharp issue with this concept. He felt the features that decisively separated the trilobites from the Crustacea were:

1. Trilobation of the dorsal shield and presence of pleura.
2. Tendency towards formation of a styliform telson.
3. Highly ramified intestinal diverticula.
4. Four postoral segments in the larva rather than two.
5. Absence of trilobite appendage in any crustacean.

He carefully documented affinities of the trilobites with the Arachnida, Eurypterida and Xiphosura and placed all these groups in the phylum Arachnomorpha. The phylum, according to Størmer, consists of two subphyla: the Chelicerata, comprising the Eurypterida, Xiphosura and Arachnida; and the Trilobitomorpha, consisting of the Trilobita and a most remarkable assemblage of excellently preserved, mid-Cambrian arthropod fossils from the Burgess Shale deposits of British Columbia.

This latter group presented great diversity in form although they all shared the trilobite limbs; the first head limb was uniramous and all the remaining appendages were biramous and identical, consisting of a seven-jointed endopodite (telopodite) and a flagellar—supposedly respiratory—exopodite (pre-epipodite). In a few forms, however, the second appendage was somewhat modified. Some of these fossils showed affinities with the merostomes while others, at least superficially, indicated crustacean relationships. In certain forms (*Burgessia, Waptia and Hymenocaris*) a carapace was present; the telson was either styliform or possessed caudal rami (*Yohoia, Waptia, Hymenocaris*); the dorsal shield had or lacked pleura; eyes were either sessile or pedunculate and the number of body segments varied widely.

Despite the fact that some of these Cambrian arthropods resembled the crustaceans in the development of a carapace, pedunculate eyes and caudal rami, Størmer (1944) contended that they conformed exactly with the trilobites and the merostomes of the same formation in the structure of the limbs and in the presence of intestinal diverticula. In fact, Størmer postulated that the Crustacea and Arachnomorpha developed independently:

> In spite of the crustacean characters exhibited in certain genera the present author is not inclined to assume an evolution of the Crustacea from groups related to the Trilobita. The chief objection to such a relationship is the complete lack of trilobitan appendages in Crustacea. Calman is obviously right in warning against putting too much weight on more isolated coincidences, or lack of coincidences in structure, but the present of the characteristic trilobitan limb in many different groups of the Arachnomorpha can hardly be regarded as an isolated coincidence. We have seen how the primitive trilobitan limb is found, more or less modified, in very different groups and traced even in terrestrial forms. It seems therefore difficult to understand why this conservative structure evidently is not preserved in any of the numerous aquatic Crustacea, not even in Devonian representatives. The peculiar development of the intestinal diverticula is, with the exception of a few parasitic copepods, apparently unknown in the Crustacea. Perhaps the most important difference between the Crustacea and Arachnomorpha is the probably different number of larval segments in the two groups.
>
> For these reasons the present author is preliminarily inclined to regard the crustacean-like members of the Trilobitomorpha as not related to the Crustacea. [Størmer, 1944]

Probably the most decisive difference is that the Burgess Shale fossils lacked mouth parts while Crustacea, in common with Insecta and Myriopoda, are mandibulates. Thus by definition these fossils were not crustaceans, although with the modification of the cephalic limbs, the Crustacea, conceivably, could have been derived from such forms.

In the light of the morphology of the Cephalocarida, how valid is Størmer's thesis? Preliminary observations of newly hatched larvae of *Hutchinsoniella* reveal that, unlike other crustaceans, at least three rather than two postoral somites are present. Yet it is questionable how significant this characteristic is, since the four postoral segments found in the trilobite

larva may have represented merely a later stage of hatching.

The pronounced ramification of the intestinal diverticula in the Arachnomorpha may be related to the absence of mouth parts. With the elaboration of these latter structures in the crustaceans, need the complexity of the gut persist? Størmer himself pointed out that intestinal diverticulae are found only in certain parasitic copepods among the crustaceans. Interestingly enough, the mouthparts are secondarily lost in these forms, although the ramification of the gut may be merely a response to the parasitic sucking habit.

Hutchinsoniella agrees with the trilobites in having a tripartite dorsal shield with well developed pleura.

Finally, *Hutchinsoniella,* in common with the Trilobitomorpha, is the only known crustacean that has a seven-jointed endopodite with gnathobases on the coxopodite. Thus this animal possesses a limb very much like that of a trilobite.

The justification for assuming that one of the so-called "terminal spines" of the cephalocarid endopodite is a dactyl might be questioned. Sectioned material reveals a muscle band entering the middle "spine" as well as the presence of a well-developed articulating membrane. Furthermore, observations on a living specimen under the microscope show occasional flexures of this same dactyl on the endopodite of the first maxilla as well as on the seven-segmented endopodite posterior to it.

The only serious discrepancy in this comparison is that the exopodite is borne distally on the protopodite rather than proximally as in the trilobites (Fig. 4). Since the protopodite of the Cephalocarida is apparently unsegmented, an increase in growth proximally coupled with a decreased rate of growth distally could displace an initially proximal exopodite to a terminal position. However, if the crustaceans arose from a common ancestor, then the limb as found in *Hutchinsoniella* represents an ideal transitional stage.

Such a view might be criticized on the basis of the trilobite limb having a precoxal segment. Snodgrass (1956), among others, questions the presence of a precoxal segment in the trilobites and sug-

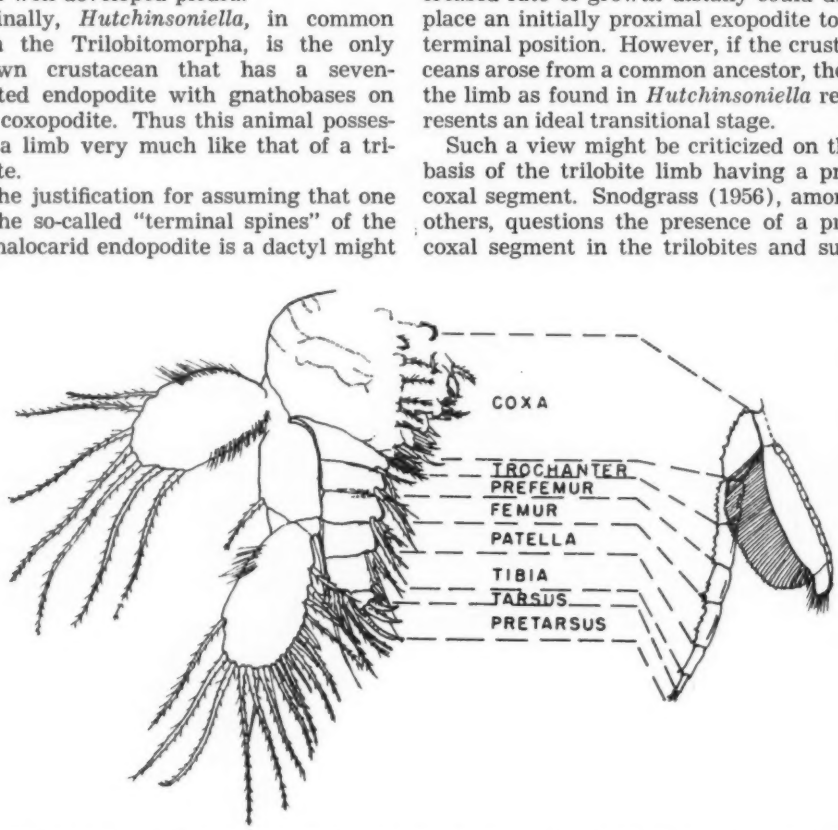

FIG. 4. A comparison of the trilobite (right, *Neolonus serratus,* adapted from Størmer, 1939) and cephalocarid limbs.

gests that the narrow "precoxa" may merely be an internally strengthened ridge for muscle attachment. Concerning the number of segments present in the arthropod limb, he states "If all the podomeres in the legs of the trilobite . . . are true musculated segments, the ancient arthropods had eight limb segments, including a small apical dactylopodite . . . and thus possessed all the segments that are present in any of the legs of modern arthropods. Among the latter, eight segments are present in Pycnogonida and in the legs of the arachnid Solpugidae. . . . The legs of the chilopods and the decapods have seven segments; the insect leg has only six segments. . . ." Therefore *Hutchinsoniella* is the only known mandibulate that retains the primitive arthropod eight-segmented limb pattern.

It is conceivable that the triramous cephalocarid appendage may more closely approximate the limb of the arthropod ancestor than the trilobite appendage does. In such a case the trilobite exopodite would be homologous to either the cephalocarid exopodite or pseudepipodite. Possibly the protocrustacean exoskeleton was only slightly calcified as is the case in modern mysids. In contrast to the trilobites, there is little likelihood that such animals would leave a fossil record. Certainly if one assumes an annelid ancestry for the arthropods, the Crustacea and particularly the Cephalocarida, come closer in approximating such a form than did the trilobites on the basis of a more vermiform shape and the position of the anus. Whatever the true situation may be, the cephalocarid limb does indicate that the Crustacea and the Trilobita were not independently derived.

The evidence obtained from the external anatomy of *Hutchinsoniella macracantha* would seem to indicate that the early crustaceans could have readily been derived from forms similar to the mid-Cambrian pseudocrustaceans.

The evidence of true crustacean remains during the Paleozoic era are few and widely scattered. Triebel (1941) obtained valves with muscle scars from supposed ostracods from the late Silurian. Such information is of little value to this study since none of the anatomy had been preserved.

Brioli (1928) described an obvious malacostracan, *Nahecaris Sturtzi*, with clearly defined first and second antennae, an eight-segmented abdomen and a definite caudal furca from the early Devonian Hunsdruck Shale of Germany. Its relationship to the extant order Leptostraca seems evident, although the abdominal segments are reduced to seven in the latter.

By far the best documented of the early fossil crustaceans is the mid-Devonian *Lepidocaris rhyniensis* described by Scourfield (1926) from the Rhynie Chert deposits of Scotland. The affinities of this animal to the Branchiopoda, particularly the order Anostraca, are striking. It possessed the naupliar first and second antennae of that group, as well as palpless mandibles, reduced first maxillae, a cervical groove, foliaceous limbs with gnathobases on the first three trunk segments, and lacked a dorsal carapace. *Lepidocaris* most probably was related to the forms that gave rise to the modern branchiopodans.

Despite this, the similarities between *Lepidocaris* and *Hutchinsoniella* are conspicuous in the overall length of 3 mm, the general form and the presence of pleura (Fig. 5). Both forms agree in having gnathobases on some (*Lepidocaris*) or all (*Hutchinsoniella*) of their trunk appendages. The first maxilla in *Lepidocaris* is highly reminiscent of the gnathic process of the biramous first maxilla of the adult *Hutchinsoniella*.

The extreme primitiveness of *Lepidocaris* is demonstrated by the fact that it maintained the masticatory process on the second antenna almost to the adult stage, a structure present only in the nauplii of the branchiopods, copepods and cirripedes. The only other known crustacean where such a masticatory process is retained to such a late stage is *Hutchinsoniella* (see Fig. 7, *B*).

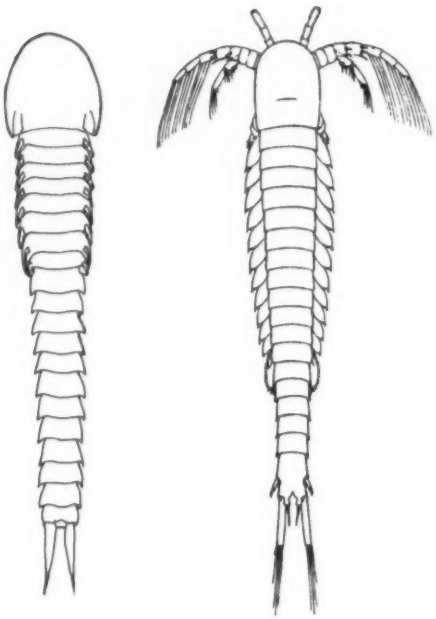

FIG. 5. The extant *Hutchinsoniella macracantha* (left) and the mid-Devonian fossil, *Lepidocaris rhyniensis* (right, after Scourfield, 1926).

Remane, on the basis of the original description of *Hutchinsoniella,* was so impressed by the similarities of these two animals that he suggested in a recent paper (1956)

> Fast könnte man versucht sein, *Lepidocaris* mit *Hutchinsoniella* in die Ordnung der Cephalocarida einzureihen, dann wäre *Hutchinsoniella* ein rezenter Vertreter einer bisher fossil aus dem Paläozoikum bekannten Ordnung, und eine Zeitungsnotiz hätte Recht, nach der dieser Fund ebenso wichtig wäre wie des berühmten Fisches *Latimeria.*

Thus despite the 300 million years that separate these two forms, it is apparent that *Lepidocaris* represents the closest known relative of the extant cephalocarid, *Hutchinsoniella macracantha,* and yet the living species must be considered the more primitive due to its only slightly modified first maxilla, the wholly unmodified second maxilla and its trilobite-like appendages.

Derivation of the Crustacean Trunk Limbs

Because of the large number of distinctive morphological characters common to both these forms, it might prove profitable to compare the thoracic appendages closely. On casual observation they seem widely different; in the Devonian form there is a gradual change from unmistakable foliaceous anterior appendages with gnathobases to copepodan biramous limbs lacking gnathobases on the posterior thorax; while the cephalocarid limb is trilobite-like with a seven-jointed walking endopodite, an exopodite consisting of two large flattened segments separated by a small articulating joint, and an oar-like flattened pseudepipodite.

Yet, if the endopodite in the cephalocarid limb were lost, the resultant appendage would be almost identical with the second and third trunk limbs of *Lepidocaris.* This does actually occur in the eighth postcephalic limb of *Hutchinsoniella* (Fig. 3, *D*).

It is therefore possible to trace by a continuous series of steps the evolution of the trilobite limb as found in the cephalocarid to the foliaceous on one hand (Fig. 6, *1* to *5*), and the biramous copepodan on the other (Fig. 6, *1, 2, 3, 6, 7*). With a reduction of a single segment in the endopodite and a loss of the gnathic processes on the coxa, the cephalocarid appendage can be converted into a limb characteristic of the primitive Malacostraca (*8*). In the primitive Leptostraca we find appendages that are highly reminiscent of the cephalocaridan plan. Again the cephalocarid endopodite together with gnathobases, is reflected in the second maxilla of a larval penaeid shrimp * (*9*).

One might justifiably criticize the derivation of a two-jointed protopodite as exemplified by *Nebalia* from an unjointed cephalocarid protopodite. Therefore it may be necessary to postulate an appendage that is similar in every way to the

* In a very recent paper (1957) Heegaard observed that both an exopod and pseudexopod form and later coalesce with part of the basis during the development of the second maxilla in a number of decapods. Such a stage can be interpreted as having the homologous parts of the cephalocarid appendage.

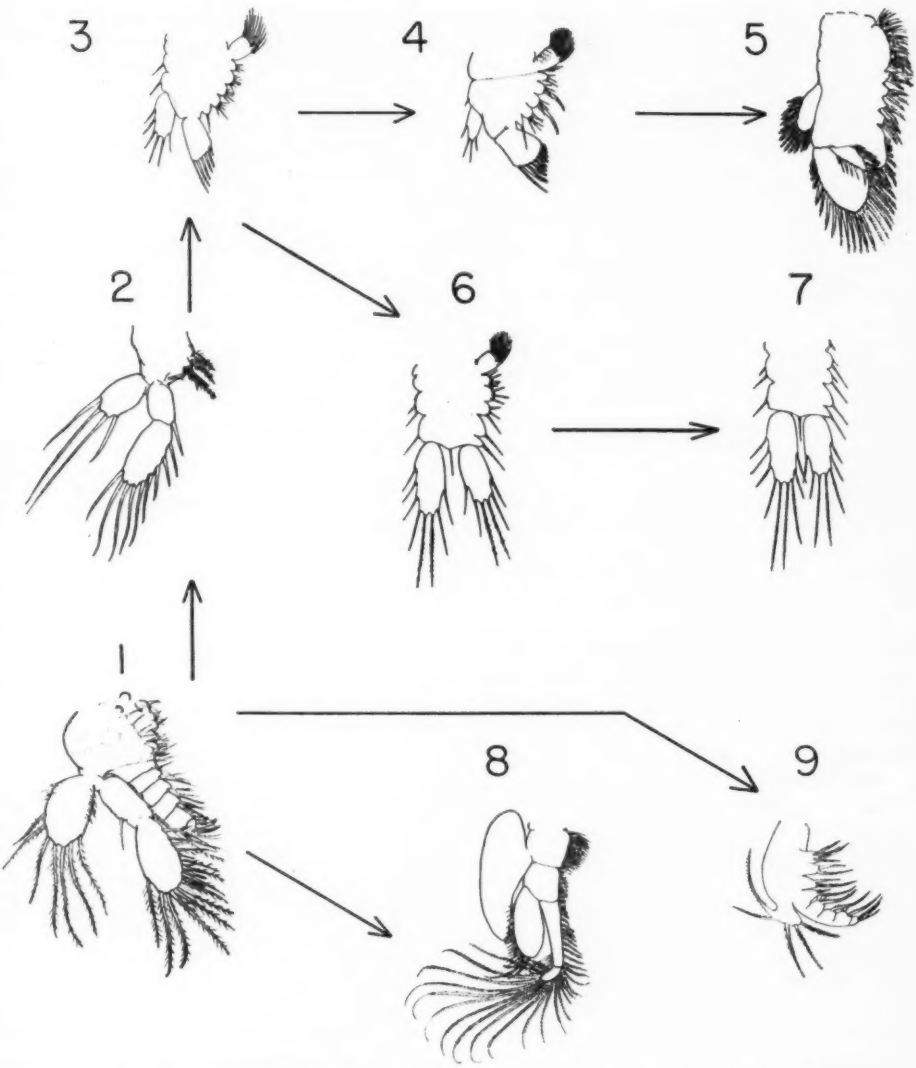

FIG. 6. Scheme showing the possible evolution of the various crustacean appendages from the cephalocarid limb. *1*, fourth thoracic appendage of *Hutchinsoniella*. *2*, eighth thoracic appendage of *Hutchinsoniella*. *3*, second or third thoracic limb of *Lepidocaris* (Scourfield, 1926). *4*, first thoracic limb of *Lepidocaris* (Scourfield, 1926). *5*, foliaceous thoracic appendage of *Branchionecta paludosa* (redrawn from G. O. Sars, 1896). *6*, fourth to sixth(?) trunk limb of *Lepidocaris* (Scourfield, 1926). *7*, biramous copepodan seventh(?) to eleventh trunk limb of *Lepidocaris* (Scourfield, 1926). *8*, malacostracan thoracic appendage as exemplified by *Nebalia bipes* (redrawn from G. O. Sars, 1896). *9*, second maxilla of a penaeid larva (Claus, 1886). All limbs oriented with endopodite on the right.

cephalocarid limb except that a basipodite is present which separates the exopodite from the pseudepipodite. Such a limb could readily serve as a precursor to the primitive malacostracan appendage. However, this writer can see no objection to the concept of a jointed protopodite evolving from an unjointed one if granted adequate time. For example, the elongation of an unjointed protopodite may make it functionally feasible for an additional segment or two to develop within the protopodite.

This scheme indicates that all known basic types of crustacean limbs could have evolved from an appendage similar to the modern cephalocarid limb which, in itself, is a slightly modified trilobite appendage. Comparing the foliaceous and cephalocarid limbs, (Fig. 6, *5* and *1*), it is apparent that the flabellum is homologous to the pseudepipodite and the apical lobe is derived from the exopodite. Regarding the copepodan type of appendage, the exopodite can be derived from the pseudepipodite and the endopodite from the cephalocarid exopodite (*7* and *1*). Only when contrasting the malacostracan and cephalocarid limbs are the endopodites and exopodites directly homologous (*1* and *8*).

There is one perplexing aspect to this proposed plan of evolution, that is, why should the so-called primitive appendage as exemplified by the Cephalocarida be more complex in structure than the limbs derived from it? In other words, has evolution in regard to the crustacean limb consisted of reduction and simplification? The Arachnomorpha generally have complicated appendages with complex gnathic processes and spines. Among the Trilobitomorpha all appendages except the first antenna had both a trophic and motile function with no limb specialized for any one specific purpose. With the alteration of the mandibles and the first and second maxillae primarily for feeding in the crustaceans, there has been a corresponding modification of the natatory parts as well as a tendency to lose the trophic function of the postcephalic appendages. Trunk limbs that have gnathobases are found today only in the foliaceous appendage of the branchiopods and in the cephalocarids as represented by *Hutchinsoniella*.

Serial Homologies

Observations on living specimens of *Hutchinsoniella* indicate that all limbs have two functions: the first and second antennae, besides the usual sensory function, are utilized in swimming and crawling; each of the remaining limbs is used jointly for locomotion and feeding. The limb movements are metachronal.

All appendages in *Hutchinsoniella*, including the first antenna, are biramous, and if one is inclined to regard as additional rami the pseudepipodite on the thoracic legs, the long gnathic structure on the first maxilla and the masticatory process on the second antenna, then such appendages can be considered triramous. There is one limb, however, that departs widely from this generalized limb pattern and that is the highly reduced, palpless, mandible (Fig. 1, *E*).

Due to the sharp deviation in plan exhibited by the mandible in the adult, it was thought advisable to study a younger stage. Two animals were examined from a juvenile stage with ten postcephalic segments and three postcephalic limbs. The figures of the head appendages are shown in Figure 7. Several things are immediately evident from the illustrations. The mandible at this stage (Fig. 7, *D*) bears a palp made up of a six-jointed exopodite and a bifurcated endopodite; the appearance of the limb is not unlike the same structure in the calanoid copepods. The first antenna (Fig. 7, *A*) is similar to that of the adult, although the flagellum (the articulating knob) is more prominent. This structure somewhat resembles the first antenna of the syncarid malacostracan *Bathynella* (see Siewing, 1956). The exopodite of the second antenna (Fig. 7, *B*) is relatively less massive than in the adult and the setae seem to be restricted to the medial and distal surfaces. A prominent masticatory process is present at the base of the appendage (Fig. 7, *C*). The maxilla (Fig. 7, *E*) appears to lack the large

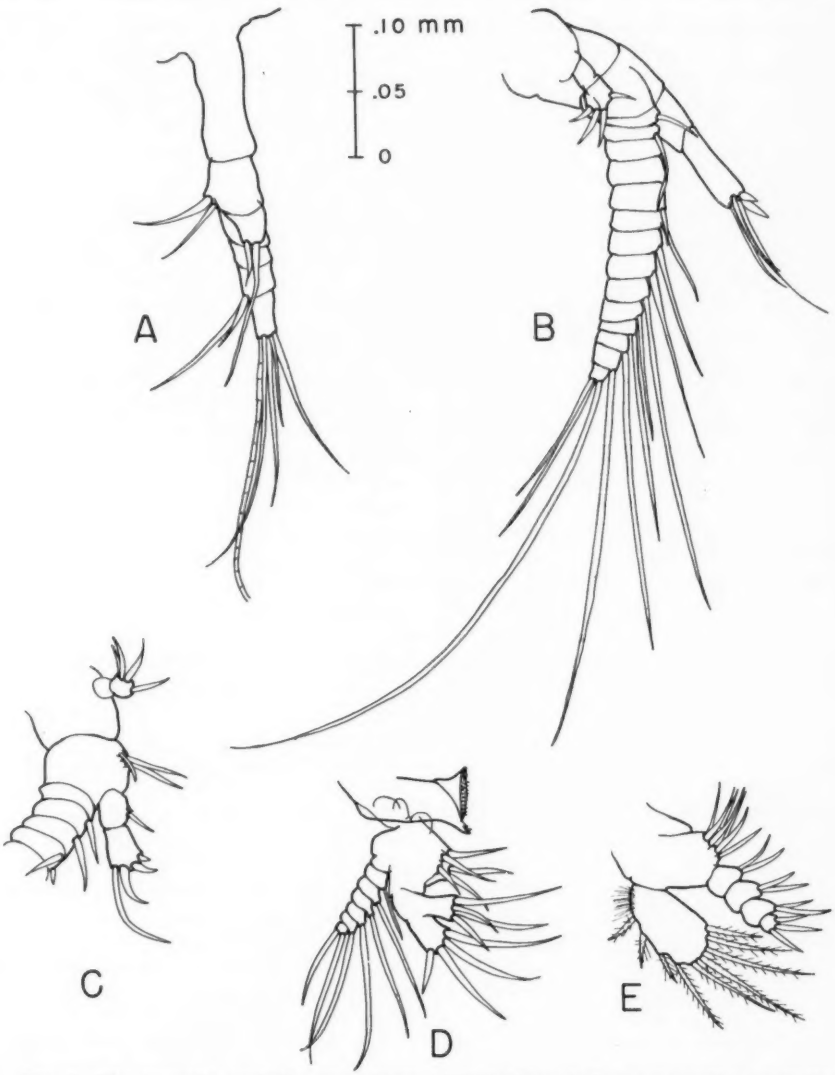

FIG. 7. The juvenile cephalic appendages of *Hutchinsoniella macracantha*, excluding the second maxilla. *A*, first antenna. *B*, second antenna. *C*, base of second antenna, showing gnathic spines between endopodite and masticatory process. *D*, mandible. *E*, first maxilla. Limbs oriented with endopodite on the right.

gnathic process found in the adult, but instead has gnathic spines on the protopodite. Similar spines on the same part of the limb are present on the mandible (Fig. 7, *D*) and the second antenna (Fig. 7, *C*). It is highly probable that these structures, because of their function and location, are homologous to the gnathobases of the thoracic limbs. The second antenna and mandible are remarkably alike; one is inclined to feel that the masticatory processes (which largely makes

up the adult mandible) proximally located on the limbs are homologous structures.

It should be mentioned at this point that the second maxilla in both the adult and juvenile is similar in appearance to the trunk limb series. No limb rudiment appears in the ontogeny of *Hutchinsoniella* between this appendage and the first maxilla. In those cases where the second maxilla is secondarily lost in the Crustacea, the first maxilla is appreciably reduced. On the other hand, *Hutchinsoniella* possesses the least modified first maxilla of any known crustacean. It is most probable that *Hutchinsoniella* represents a stage in the evolution of the crustaceans wherein the last cephalic limb represents the as yet unmodified precursor of the second maxilla as found in the other groups.

This study indicates a common basic limb-pattern and implies a strong serial homology among all appendages, excepting, perhaps, the first antenna. Within this limb plan two subseries seem evident: the second antenna and mandible with a many-jointed exopodite, and the first and second maxillae and the trunk limbs with a many-jointed endopodite. It is of some interest that the biramous limb-structure plan with gnathic spines on the coxal segment was precisely the scheme found in the Trilobitomorpha.

Homology of the Cephalic Limbs

How similar are these juvenile cephalic appendages to the same structures in the other crustacean groups? Can a common basic plan be detected in those subclasses where the head appendages have not been markedly modified? The calanoid copepod, *Paracalanus parvus* as described by Sars (1903, Plate VIII) and the cladocopan ostracod, *Polycope punctata* (Sars, 1928, Plate XV) were selected for this comparison. Both of these forms are usually thought of as being representative of the more primitive elements within their subclasses. In addition, the type species of the subclass Mystacocarida, *Derocheilocaris typicus* (Pennak and Zinn, 1943, Plate 2) and the nauplius stage of the barnacle, *Balanus trigonus* (Sandison, 1954, fig. 6) were also included. The second antenna, mandible and first maxilla of these animals, together with the same juvenile head structures of *Hutchinsoniella,* are figured in Figure 8.

The second antennae are remarkably alike in all groups, consisting of an exopodite of numerous segments, each giving rise to a single long seta and the apical joint which bears two or three setae. Except for *Derocheilocaris,* these long setae insert on the inner aspect of the ramus, although Dahl (1952) figures the second antenna in *D. galvarini* with setae on the medial edge. The endopodite always consists of fewer segments than the exopodite. In those forms where the juvenile stages are figured (*Hutchinsoniella, Derocheilocaris* and *Balanus*) the masticatory process is clearly evident.

The mandibles of these widely separated crustaceans show pronounced morphological similarity and, at the same time, bear strong structural resemblance to the second antennae. The exopodite, except in the case of the ostracod representative, consists of numerous segments, with the joints in most cases supporting a single long seta on their inner margins. The endopodite is made up of fewer segments. Gnathic spines are present on the medial aspect of the protopodite although this is less apparent in *Derocheilocaris.*

The first maxilla shows more diversity. The cephalocarid limb seems to be the least modified, having as it does a five-jointed endopodite, a single-jointed flat exopodite, and gnathic processes on the protopodite. This same scheme can be detected in the copepodan and ostracod maxillae, although there is an evident reduction of the endopodite segments and a general fusion of the limb. In the Mystacocarida the exopodite disappears. The first maxilla is not yet formed in the cirripede nauplius.

The comparison reveals remarkable similarity in the cephalic appendages of some of the less specialized representatives of five crustacean subclasses. Among these animals, *Hutchinsoniella* must be

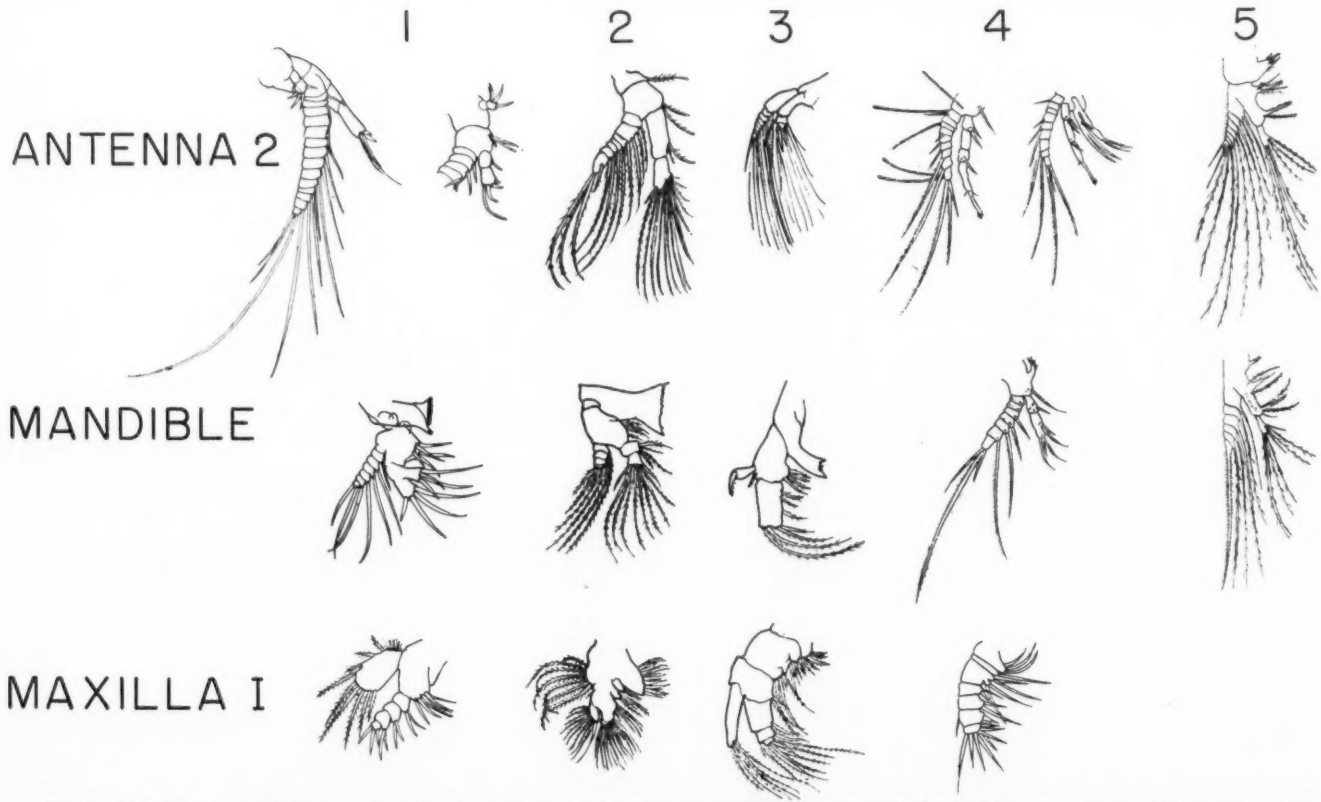

FIG. 8. A comparison of the second antenna, mandible and first maxilla among representatives of five crustacean subclasses. *1.* Juvenile limbs of the cephalocarid, *Hutchinsoniella macracantha.* *2.* Adult appendages of the calanoid copepod, *Paracalanus parvus* (redrawn from Sars, 1903). *3.* Adult limbs of the cladocopan ostracod, *Polycope punctata* (redrawn from Sars, 1928). *4.* Appendages of the mystacocaridan, *Derocheilocaris typicus;* antenna 2 on right is juvenile structure (Pennak and Zinn, 1943). *5.* Naupliar appendages of the cirripedian, *Balanus trigonus* (Sandison, 1954). All limbs oriented with endopodite on the right.

considered as more closely approximating the primitive condition primarily because of the generalized first and second maxillae.

Hutchinsoniella *and the Crustacean Ancestor*

How does *Hutchinsoniella* compare with the hypothetical crustacean ancestor as interpreted by various morphologists? MacBride (1914) stated

> We can now form a picture of the course which evolution followed in transforming the ancestor represented by a Nauplius to a primitive crustacean. The second antenna became gradually shifted forward and lost its masticatory function, while the third appendage became exclusively masticatory and its distal joints shrank to an insignificant palp. At this stage of evolution the animal was assisted in mastication by the modification of the appendage of the next two or three segments, which formed maxillae, but which were never greatly changed from their original parapodia-like condition.

Except for MacBride's belief that the foliaceous trunk limb was the primitive appendage, and the almost unmodified condition of the first and second maxillae in *Hutchinsoniella,* there is no great discrepancy between his prototype and the extant cephalocarid.

The "Urphyllopod" or original crustacean of Claus (1876) was thought to have a mandibular foot and more strongly developed foot-like maxillae. The second antennae were considered to be used in locomotion and feeding and "sie besassen die kräftigen Mundhaken und eine Gestaltung, wie sie in der Larvenzeit des Copepodon, Cirripedien und Phyllopoden so überraschend ähnlich sich wiederhalt." The trunk limbs were considered as being "im Einzelen selbst sehr verschieden gestalteten Phyllopodenfüssen und den Spaltfüssen der Schizopoden standen." The cephalocarid limb, with gnathobases on a mixopodium, has components of both the phyllopod and biramous appendage. *Hutchinsoniella* has, almost to the adult stage, a second antenna and mandible that are utilized both in locomotion and food manipulation. Furthermore, the cephalocarid first maxilla is indeed foot-like, and the second maxilla is almost identical to the trunk limbs.

Calman (1909) wrote

> In order to reconstruct the hypothetical ancestral type, therefore, it is necessary to combine the characters of several existing groups. It may be supposed to have approximated, in general form, to Apus, with an elongated body of numerous similar somites, terminating in a caudal furca; with the postoral appendages all similar, and with a carapace originating as a shell-fold from the maxillary region. The eyes were probably stalked and movable, the antennules uniramous, and the antennae and mandibles biramous and natatory, and both armed with masticatory processes. The trunk limbs were probably biramous but with additional endites and exites, and all provided with gnathobases.

It is questionable whether the stalked eyes are a primitive condition, and neglecting the first antenna, *Hutchinsoniella* readily approximates Calman's hypothetical ancestral type.

After carefully surveying the various major crustacean groups, Dahl (1956) concluded "the evidence brought forward . . . indicates that the Crustacea, and probably other Arthropods as well, had originally a ventral mouth, more or less ventral (antennae and) antennulae and a more or less straight central nervous system. Any other supposed arrangement will be inconsistant with the morphological facts." This description can be applied directly to *Hutchinsoniella.*

It is evident that *Hutchinsoniella macracantha* comes remarkably close to these interpretations of the crustacean ancestor. Can this cephalocarid be regarded as an extremely primitive living fossil?

Crustacean Phylogeny

Some mention must be made of the important contribution by Dahl (1956*a*) to the understanding of crustacean phylogeny based on studies of the Mystacocarida and the Cephalocarida. He designates and characterizes four crustacean subclasses: Ostracoda; Malacostraca; Gnathostraca (including the orders Cephalocarida, Anostraca, and Phyllopoda); and Maxillopoda (containing the orders Mys-

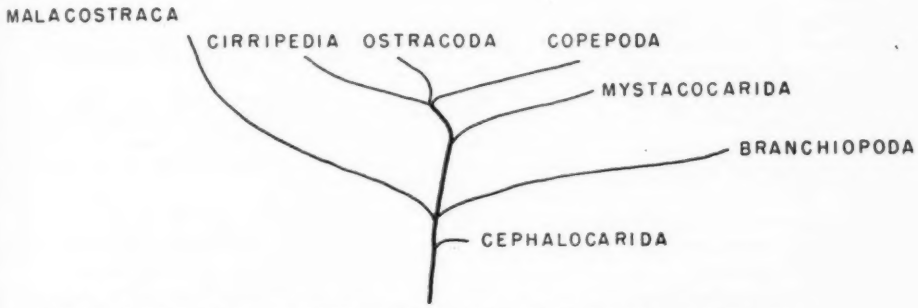

FIG. 9. A proposed scheme showing the evolution of the crustacean subclasses.

tacocarida, Archicopepoda, Copepoda, Branchiura and possibly the Cirripedia). He is quite correct in pointing out that

> Undoubtedly the discovery of the Mystacocarida and the Cephalocarida brought the Anostraca and the Copepoda closer to each other. Within the series Euanostraca–Lipostraca–Cephalocarida the general resemblance to the Copepoda increases step by step. In a similar way it could be said that the Mystacocarida at least in their internal organisation are not as far removed from the Anostraca as are the Copepoda. . . . But although the gap between the Anostraca and the Copepoda is not as wide as it used to be it seems impossible to say that the discovery of the two new crustacean groups obliterated the limits between the two evolutionary lines. It seems probable that they were derived from a common ancestor but it appears certain that they branched off in different directions at an early phylogenetic stage.

The information available to Dahl concerning the Cephalocarida was limited to the original description (Sanders, 1955). According to Dahl's classification, additional morphological details in the present paper indicate that *Hutchinsoniella* has the head of a maxillopodan, the body of a gnathostracan but with thoracic limbs not far removed from those of a trilobite. This writer feels that the two evolutionary lines do converge within the Cephalocarida.

On the basis of the comparative morphology presented in this paper, the author proposes a possible scheme of crustacean affinities (Fig. 9). The Cephalocarida must be placed close to the main stem of crustacean evolution since it uniquely retains the naupliar masticatory process on the second antenna, the only slightly modified trilobite appendage, and a second maxilla that is unaltered from the trunk limb pattern.

The characters that are common to both the Cephalocarida and Branchiopoda are the numerous body segments, the retention of gnathic processes on the trunk limbs and a paired ventral nerve cord. Evolution in a branchiopodan direction would consist of a modification of the cephalocarid trunk limb to the foliaceous limb and a pronounced reduction of all head appendages.

The primitive malacostracan thoracic limb can be directly homologized with the cephalocarid trunk appendage and both groups have a biramous first antenna. A reduction in body segments, the loss of gnathic processes on the trunk limbs and a modification of the mouth appendages were the components of malacostracan evolution.

The generalized head appendages are shared by the Cephalocarida with the Copepoda, Ostracoda, the nauplii of the Cirripedia, and the Mystacocarida. There has been a reduction of trunk segments, a loss of gnathic processes on the trunk limbs and a conversion of the cephalocarid appendage to a biramous copepodan limb or to a mere rudiment as is the case in the Mystacocarida. This latter group, however, has retained the paired ventral nerve cord (Dahl, 1952).

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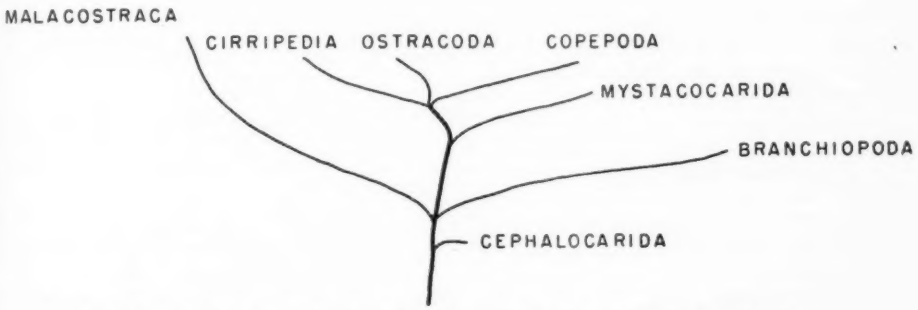

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Viewing the morphology of *Hutchinsoniella* on the basis of the entire complex of arthropods, extinct and extant, one is left with the impression that the present day cephalocaridan is not far removed from the ancestral crustacean stock that probably existed during the Silurian or earlier. This impression is based on its apparent affinities to the trilobites, the close relationship between it and the mid-Devonian fossil *Lepidocaris*, and the morphological characters it shares with the more primitive members of the various extant crustacean groups.

Finally, the evidence strongly refutes the polyphyletic origin of the crustaceans suggested by certain investigators such as Garstang and Gurney (1938), and the primitiveness of the foliaceous appendage as advanced by MacBride (1914) and Borradaile (1926). The validity of Størmer's phylum Arachnomorpha as a natural group can be seriously questioned since a concise evolutionary sequence can be traced from certain Trilobitomorpha present in the mid-Cambrian Burgess Shale deposits through a cephalocarid-like intermediary to the other present day crustacean subclasses.

BIBLIOGRAPHY

BORRADAILE, L. A. 1926. Notes on crustacean limbs. *Ann. Mag. Nat. Hist., London,* Ser. 9, *17*:193–213.

BRIOLI, F. 1928. Beobachtungen an Nahecaris. *Sitzungsber. M.-N. Abt. Bayerische Akad. Wiss.*, 1–18.

CALMAN, W. T. 1909. Crustacea, in Sir Ray Lankester (Ed.), *A Treatise on Zoology,* Part VII, fasc. 3.

CLAUS, C. 1876. Untersuchungen zur Erforschung der genealogischen Grundlage des Crustaceen-Systems. 4 to. Wien.

——— 1886. Neue Beitrage zur Morphologie der Crustacean. *Arb. Zool. Inst. Wien, 6*:1–108.

DAHL, E. 1952. Mystacocarida, con resumen en español. Reports of the Lund University Chile Expedition 1948-49, No. 7. *Lund Univ. Arrsk. N.F. Avd., 2, 48*:1–40.

——— 1956. On the differentiation of the topography of the Crustacean head. *Acta Zoologica, 37*:123–192.

——— 1956*a*. Some crustacean relationships. Bertil Hanström, *Zoological papers in honor of his sixty-fifth birthday November 20, 1956:* 138–147.

GARSTANG, W., and GURNEY, R. 1938. The descent of the Crustacea from trilobites, and their larval relations. In: *Evolution, Essays presented to E. S. Goodrich,* G. R. deBeer, Ed.: 271–286.

HEEGAARD, P. 1957. The second maxilla in the Decapoda. *Ann. Zool., 2*(3):39–46.

MACBRIDE, E. W. 1914. Text-book of embryology. Vol. 1. Invertebrata. London.

PENNAK, R. W., and ZINN, D. J. 1943. Mystacocarida, a new order of Crustacea from intertidal beaches in Massachusetts and Connecticut. *Smithsonian Misc. Coll., 103*(9):1–11.

REMANE, A. 1956. Die Cephalocarida, eine weitere neue Ordnung (Unterklasse) der Krebse. *Mikrokosmos, 45*:227–230.

SANDERS, H. L. 1955. The Cephalocarida, a new subclass of Crustacea from Long Island Sound. Proc. Nat. Acad. Sci., *41*(1):61–66.

SANDISON, E. E. 1954. The identification of the nauplii of some South African barnacles with notes on their life histories. *Trans. Roy. Soc. South Africa, 34*(1):69–101.

SARS, G. O. 1896. Fauna Norvegiae-Phyllocarida and Phyllopoda. Christiania. 140 pp.

——— 1903. A account of the Crustacea of Norway. 4. Copepoda. Bergen Museum. 171 pp.

——— 1928. An account of the Crustacea of Norway. 9. Ostracoda. Bergen Museum, 277 pp.

SCOURFIELD, D. J. 1926. On a new type of crustacean from the Old Red Sandstone (Rhynie Chert bed, Aberdeenshire), *Lepidocaris rhyniensis* gen, et sp. nov. *Phil. Trans. Roy. Soc. London, Ser. B, 214*:153–187.

SIEWING, R. 1956. *Thermobathynella amyxi* nov. spec. aus dem Brackwasser der Amazonasmündung. *Kieler Meeresforsch., 12*:114–119.

SNODGRASS, R. E. 1956. Crustacean metamorphoses. *Smithsonian Misc. Coll., 131* (10):1–78.

STØRMER, L. 1939. Studies on trilobite morphology. I. The thoracic appendages and their phylogenetic significance. *Norsk geol. tidsskr., 19*:143–274.

——— 1942. Studies on trilobite morphology. II. The larval development, the segmentation and the sutures, and their bearing on trilobite classification. *Norsk. geol. tidsskr., 21*:49–163.

(*Concluded on page 148*)

Historical Notes on Avian Classification

BARBARA G. BEDDALL

THE first scientific classification of birds appeared in 1676 in the *Ornithologiae* of Francis Willughby and John Ray. This remarkably successful scheme was the first to characterize small, homogeneous groups of birds so that accurate identification was possible. But, just as there is always a history preceding a milestone, the beginnings of bird classification can be traced back to Aristotle (384-322 B.C.), the father of natural history. His zoological writings are the first that have survived to our times, although he represents the culmination of Greek science, not its beginning.

Classical Accounts

Aristotle collected all the contemporary knowledge of animal life and added his own personal observations. He was not primarily interested in birds nor did he make a formal classification of animals. Yet in his *Historia Animalium* he mentioned about 170 species of birds, a large number of which can be identified today, and he made several important contributions to the subject of classification.

"Animals differ from one another in their modes of subsistence, in their actions, in their habits, and in their parts. . . . For instance, some animals live in water and others on land" (Aristotle/Thompson, 1910: p. 487*a*). "The whole genus of birds may be pretty well divided into such as procure their food on dry land, such as frequent rivers and lakes, and such as live on or by the sea" (Aristotle/Thompson, 1910: p. 593*a*). The classical division between land and water birds survived as a primary distinction in ornithological classification until Linnaeus, and these biological characteristics were used in the desultory attempts at classification that were made before the essentially morphological scheme of Willughby and Ray. Linnaeus and subsequent workers relied on structure alone. But Aristotle's sentence has a modern ring, for the twentieth century has seen the renewed use of biological characters as an aid in classification.

In regard to structure Aristotle wrote: "In the first place we must look to the constituent parts of animals. For it is in a way relative to these parts, first and foremost, that animals in their entirety differ from one another: either in the fact that some have this or that, while they have not that or this; or by peculiarities of position or of arrangement; or by the differences that have been previously mentioned, depending upon diversity of form, on excess or defect in this or that particular, on analogy, or on contrasts of the accidental qualities" (Aristotle/Thompson, 1910: p. 491*a*).

Plato and his pupil Aristotle recognized two systematic categories, *eidos* and *genos*. These are often translated as species and genus. *Eidos* is more or less comparable to species, although occasionally applied to small groups; but *genos* refers to a combination or group usually of the degree of the present-day class, order or family. For instance, "Creatures that have feathered wings are classed as a genus under the name of 'bird' " (Aristotle/Thompson, 1910: p. 490*a*). "Very extensive genera of animals, into which other subdivisions fall, are the following: one, of birds; one, of fishes; and another, of cetaceans" (Aristotle/Thompson, 1910: p. 490*b*).

Aristotle never outlined a system of

classification, if, indeed, he actually had one in mind. But he did characterize animals and groups of animals in such a way that later authors have constructed a system from his writings. Naturally, interpretations vary. There seem to be two principal points of view about his groups of birds.

Three leading ornithological scholars, Alfred Newton (1896: p. 3), A. H. Evans (1903: p. 40) and Erwin Stresemann (1951: p. 2) list these eight different groups of birds: (1) Gampsonyches (crooked claws), which are carnivorous and are roughly equivalent to the Accipitres of Linnaeus; (2) Scolecophaga (worm-eating), including most of the Oscines except for the (3) Acanthophaga (thistle seed-eating), goldfinch, siskin and a few others; (4) Scnipophaga (grub-eating), the woodpeckers, including the nuthatch; (5) Peristeroide (dove-like), pigeons and doves, which eat fruit and herbage; (6) Schizopoda (cloven-footed), a collection of cloven-footed water birds, roughly equivalent to the Grallae of Linnaeus; (7) Steganopoda (web-footed), swimming birds, roughly equivalent to the Anseres of Linnaeus; (8) Barea (heavy), ground birds, roughly equivalent to the Gallinae of Linnaeus. As a matter of fact, Linnaeus was well acquainted with Aristotle, his father having given him a copy of the *Historia Animalium* when Linnaeus was a student.

Charles Singer (1931: p. 42), the biological historian, and Thomas Lones (1912: p. 214) list these five main groups: (1) Gampsonyches, birds of prey with talons; (2) Steganopodes, swimming birds with webbed feet; (3) Peristeroeide, pigeons and doves; (4) Apodes, swifts, martins and swallows; (5) all other birds.

The following idea took the fancy of several sixteenth and seventeenth century writers. "Of birds, some take a dust-bath by rolling in dust, some take a water-bath, and some take neither the one bath nor the other. Birds that do not fly but keep on the ground take the dust-bath, as for instance the hen, the partridge, the francolin, the crested lark, the pheasant; some of the straight-taloned birds, and such as live on the banks of a river, in marshes, or by the sea, take a water-bath; some birds take both the dust-bath and the water-bath, as for instance the pigeon and the sparrow; of the crooked-taloned birds the greater part take neither the one bath nor the other" (Aristotle/Thompson, 1910: p. 633*a*–*b*). Pierre Belon mentioned different bathing habits, and both Ulisse Aldrovandi and Walter Charleton used these habits in their classifications.

It is in Rome, three hundred years later, that we find the next writer of zoological importance, the indefatigable Pliny (23-79 A.D.). His *Historia Naturalis* became one of the most famous and widely read works of his time and of the Middle Ages. It is an encyclopedia covering the entire knowledge of nature at that time, compiled from all the sources available to him including Aristotle. There has been a good deal of debate as to the value of Pliny's work. In any case, most of Book X of the 37 volumes is devoted to birds. As he customarily mentioned the largest and most remarkable animals first, he began it with the ostrich.

As far as birds were concerned, Pliny thought the formation of their feet provided the most distinguishing characteristic. Chapter XI of Book X gives his "general division of Foules. The first and principal difference and distinction in birds, is taken from their feet: for they have either hooked Tallons, as Hawkes; or round long clawes, as Hennes; or else they be broad, flat and whole-footed, as Geese and all the sort manner of water-foule" (Pliny/Holland, 1635: Vol. I, p. 276).

During the Dark Ages when scientific research and direct observation vanished from the western world, Pliny and other early writers were copied and recopied in the monasteries, while Greek natural science was condemned by the Christians as being of pagan origin. Aristotle might have been lost entirely had not Greek

science been transferred to the Arabians by a Christian sect, the Nestorians, which was driven from Alexandria as a result of religious disagreements. The Mohammedans welcomed them and permitted them to establish schools in which Greek learning was taught. Thus the Greek manuscripts were passed on to the Arabians, who translated them into their own languages. The further translation of these works into Latin began in the eleventh century, the biological works of Aristotle being so translated early in the thirteenth century by Michael Scot, the court astrologer of Frederick II who himself did some notable work on birds. Aristotle was soon looked to by the western world as an authority on natural science. He and Pliny were constantly referred to during the Renaissance and both of them exerted a good deal of influence on the thinking of that period.

The Sixteenth Century

William Turner's *Avium Praecipuarum*, 1544, the first printed book on birds, was an attempt, often successful, to identify the birds mentioned by Aristotle and Pliny. Many of Turner's own excellent observations are included in this important early work. At the end he grouped the birds under "common places" (i.e. excerpts noted for ready reference) from Aristotle "that you may with certainty refer to all those birds, of which you read in their pages." Evans (1903: pp. 181–3) gives them as follows: Those having appendices: olor, anser, anas, gallinaceus, perdix, ciconia, ascalaphus, tarda, noctua, passer; those having craws: gallinaceus, palumbes, perdix, and columbus; those having wide gullets: anser, anas, gavia, cataracta, and tarda; gregarious birds: olor, the smaller anser, grus, and platea; those living on crops: palumbes, columbus, turtur, and vinago; those frequenting lakes: ardeola, albardeola, ciconia, the grey gavia, junco, cinclus, trynga, calidris, and alcedones; those frequenting the sea: alcedo, carulus, the white gavia, fulica, mergus, rupex, and cataracta; those frequenting rivers and lakes: olor, anas, phalaris, urinatrix, bosca, the webfooted corvus, either kind of anser, vulpanser, capella, penelops, the sea aquila, those feeding on thistles: spinus, carduelis, and aurivittis; those feeding on insects: pici martii, galgulus, culicilega; those feeding on worms, either wholly, or for the most part: fringilla, passer, rubetra, luteola, and all the pari, ficedula, atricapilla, rubicilla, rubecula, sylvia, curuca, asylus, florus, montifringilla, regulus, and frugilega. Turner concluded this with the remark that "any one may devise more Places of this sort."

Conrad Gesner's *Historia Animalium* began publication in 1551. The profusion of illustrations, the effort to verify facts and the greater use of personal observation mark this as the starting-point of modern zoology. An immense encyclopedia, it is a compilation of information drawn from about 250 earlier writers and from numerous correspondents in various countries, one of whom was William Turner, and with the addition of observations made by Gesner himself. The volume on birds appeared in 1555. Gesner did not attempt a classification but adopted the alphabetical arrangement in frequent use since the second century. This was not strictly observed, however, for he grouped several obviously related forms together: hawks and falcons, ducks, gallinaceous birds.

The year 1555 also saw the appearance of Pierre Belon's *L'Histoire de la Nature des Oyseaux*. The book contained more original observations than Gesner's, and it was also extensively illustrated. There was a definite arrangement of birds, "for if it were otherwise, everything would be in confusion" (Belon, 1555: p. 6).

Using an assortment of ecological and structural factors as criteria, Belon divided birds into the following six groups: (1) birds of prey—vultures, eagles, birds of falconry, other birds of prey, nocturnal birds; (2) river birds that have flat feet and swim on the water—swan, pelican, geese, cormorant, ducks, gulls, etc.; (3)

river birds that do not have flat feet—crane, herons, flamingo, waders, etc., and also the kingfisher and bee-eater. "Because they don't wallow in dust, like the terrestial birds . . . all of them cleanse their feathers with water; they have been named *Lotrices* in contrast to the terrestial birds which are called *Pulveratrices*." (4) Birds of the open country that nest on the ground—ostrich, bustard, francolin, pheasant, partridge, quail, etc.; (5) birds that are indifferent to where they live and eat all sorts of food—raven, rook, crow, jackdaw, woodpeckers, pigeons, blackbirds, thrush, fieldfare, etc.; (6) little birds that frequent hedges, thickets and bushes, some of which eat only worms and other little creatures, others only grain, and others a combination—nightingale, robin, wagtail, goldfinch, serin, siskin, sparrows, swallows, etc.

The delightfully descriptive phrase "flat feet" was used, Belon says, as a circumlocution for the Latin *palmipes* for which there was no simple expression in his native French. He began the groups with the largest birds, using an arrangement popularized by Pliny.

Ulisse Aldrovandi hoped to outshine Gesner with his own encyclopedia of natural history. The first three volumes, his *Ornithologiae*, were published between 1599 and 1603. He was proud of his arrangement of birds which, like Belon's, used a variety of unrelated characters. His first volume contains birds with a hard and powerful bill—birds of prey, shrike, owls, ostrich, bat, parrots, crows, roller, birds of paradise, nuthatch, wryneck, tree creeper, bee-eater, crossbill, etc. Volume II: wild birds bathing in dust—peacocks, turkey, pheasant, grouse, bustard, partridge, quail, etc.; domestic fowl bathing in dust; birds bathing in both dust and water—doves, pigeons, sparrows; baccivores— thrushes, starling, hawfinch; vermivores—wren, swallows, swift, hoopoe, titmice, wagtails, flycatchers, robin, wheatear, etc.; songbirds—nightingale, finches, larks. Volume III: palmipedes—web-footed water birds; birds that live about the water—stork, flamingo, crane, etc. As noted earlier, Aristotle had mentioned the bathing habits of birds.

Volcher Coiter, who knew Aldrovandi, published a classification of birds slightly earlier. His *De differentiis Avium* appeared in 1575. But it was part of a medical work and was for a long time unknown to naturalists. Thus its effect was small, although it has recently received attention as a historical curio. In the tabulation of his knowledge of birds, Coiter agreed with Pliny that the feet were the most distinctive character and he divided birds into fissipedes and palmipedes. He subdivided the fissipedes according to the shape of the claws and then by the position of the toes; the palmipedes according to the extent of the webbing. The swallows and birds of paradise he grouped separately as Apodes.

Walter Charleton's *Onomasticon Zoicon*, 1668, was intended to be a complete, classified list of animals, with English, Latin and Greek names. In compiling it he used, among others, Gesner, Belon and Aldrovandi. As far as birds were concerned, it can be seen that he was much influenced by Aldrovandi. The land birds are divided into (1) carnivores—birds of prey, cuckoo, parrots, ravens and crows, owls, ostrich, cassowary, bat, etc.; (2) insectivores: non-singing—woodpeckers, nuthatch, wryneck, tree creeper, bee-eater; singing—hedge sparrow, titmice, wagtails, robin, wheatear, nightingale, hoopoe, etc.; (3) granivores and phytivores: bathing in dust—peacock, pheasant, grouse, bustard, partridges, quail, etc.; bathing in dust and water—wild and domestic doves and pigeons, sparrows; singing—finches, larks; (4) baccivores: singing—thrushes, starling, hawfinch, Virginian nightingale (i.e. American cardinal), etc.

The water birds are divided into (1) palmipedes—pelican, gulls, gannet, cormorant, avocet, swan, geese, ducks, coot, etc.; (2) fissipedes: piscivores—stork, flamingo, herons, kingfishers, etc.; insec-

tivores—waders, moorhen; herbivores—cranes. Of course the flamingo is web-footed, but Belon and Aldrovandi had also been confused about this. "It is whole-footed (as Gesner rightly hath it) from whom Aldrovandus, deceived (I guess) by the Picture of it dissenting, affirms the contrary, *viz.* that it is cloven-footed" (Willughby, 1678: p. 320). There is a final section on exotic birds, divided only into land and water birds. "A sorry book" was John Ray's comment.

Willughby and Ray

The *Ornithologiae* of Francis Willughby and John Ray "Wherein All the birds hitherto known, Being reduced into a Method sutable to their Natures, are accurately described" is "the cornerstone of modern systematic ornithology," to quote Zimmer (1926: p. 677). Willughby died in 1672, four years before the date of publication, and it was Ray who put his friend's notes in order. There has been much dispute about the relative contributions of the two men to the book, but none about the contribution of the book to ornithology. There are first-hand descriptions of over two hundred birds that the authors had themselves observed, plus all the birds believed (not always correctly) to be authentic from previous writers, including, of course, Gesner, Aldrovandi and Belon, and also Marcgrave, Clusius, Hernandez, Bontius, Worm and Piso. Sorting all this out required a fineness of observation and an acuteness of judgement that separate Ray's scientific achievement from the more descriptive and literary efforts of his predecessors. The 1676 edition was written in Latin, at that time still the language of the scholars. Ray brought out an English translation, with some additions, in 1678.

Cuvier said of Ray: "The distinctive character of Ray's work consists in the clearness of his methods, which were not only more rigorous than those of any of his predecessors, but applied with greater uniformity and precision. The divisions which he introduced into the classes of quadrupeds and birds have been followed by English naturalists even to the present day; and we find evident traces of Ray's arrangement of birds in Linnaeus, Brisson, Buffon, and all authors who have written upon this class of animals" (Cuvier/Lankester, 1846: p. 106).

Stabilizing the meaning of the word *species* was an integral part of Ray's accomplishment. Even today it is a difficult term to define, but from Aristotle on it had had no certain meaning at all and was applied both to groups and to individual kinds, which could be varieties, different life stages, or sex, age and color differences. It is in his botanical writings that Ray, primarily a botanist himself, pondered the question of specific distinctness. But the results of his careful thinking are evident in the *Ornithology.* Implicit in that work is the recognition that a species includes the sex, color and age variants that make up a breeding unit.

After discussing this problem in several prefaces and papers, Ray finally wrote in his *Historia Plantarum* (1686: Vol. I, p. 40):

> In order that an inventory of plants may be begun and a classification of them correctly established, we must try to discover criteria of some sort for distinguishing what are called 'species.' After a long and considerable investigation, no surer criterion for determining species has occurred to me than distinguishing features that perpetuate themselves in propagation from seed. Thus, no matter what variations occur in the individual or the species, if they spring from the seed of one and the same plant, they are accidental variations and not such as to distinguish a species. For these variations do not perpetuate themselves in subsequent seeding. Thus, for example, we do not regard *caryophylli* with full or multiple blossoms as a species distinct from *caryophylli* with single blossoms, because the former owe their origin to the seed of the latter and if the former are sown from their own seed, they once more produce single-blossom *caryophylli.* But variations that never have as their source seed from one and the same species may finally be regarded as distinct species. Or, if you make a comparison between any two plants, plants which never spring from each other's seed and never, when their seed is sown, are transmuted one

into the other, these plants finally are distinct species.

For it is just as in animals: a difference in sex is not enough to prove a difference of species, because each sex is derived from the same seed as far as species is concerned and not infrequently from the same parents, no matter how many and how striking may be the accidental differences between them; no other proof that bull and cow, man and woman belong to the same species is required than the fact that both very frequently spring from the same parents or the same mother. Likewise in the case of plants, there is no surer index of identity of species than that of origin from the seed of one and the same plant, whether it is a matter of individuals or species. For animals that differ in species preserve their distinct species permanently; one species never springs from the seed of another nor vice versa." (Translated from the original Latin by Dr. Edmund T. Silk).

Willughby and Ray classified birds primarily according to the shape of the bill, the construction of the foot and the size of the body. Although they ignored bathing habits, they did not entirely escape their predecessors in the matter of eating habits. The division between land and water birds was retained, each main section then being divided according to the principal of dichotomy. It should be noted that in such a key-type tabulation any particular group is characterized not only by the term used directly with it, but also by the terms in the divisions preceding it. As a result, each group is provided with a short diagnosis.

". . . our main design was to illustrate the History of Birds, which is . . . in many particulars confused and obscure, by so accurately describing each kind, and observing their Characteristic and distinctive notes, that the Reader might be sure of our meaning, and upon comparing any Bird with our description not fail of discerning whether it be the described or no. Nor will it be difficult to find out any unknown Bird that shall be offered: For comparing it with the Tables first, the Characteristic notes of the *genus's* from the highest or first downward will easily guide him to the lowest *genus;* among the *Species* whereof, being not many, by comparing it also with the several descriptions the Bird may soon be found" (Willughby, 1678: Preface).

There are two of these summary tables, one for each of the two main divisions, land and water birds. The water bird table (Willughby, 1678: p. 273) is presented here as a demonstration of Willughby and Ray's remarkable acuity (Table I).[1] Modern families (Wetmore, 1951) represented in the groups follow in brackets. That real progress had been made towards a natural classification can be seen from the fact that, with certain exceptions, all those groups marked with an asterisk contain birds belonging to one family or to one order. The exceptions are marked with a dagger. A few of the birds that they never saw and about which there is some doubt or confusion have been omitted.

The exceptions noted above are of some interest. The limpkin is the only real misfit (from our point of view, not Ray's). For two centuries after Ray the jacana was most often classed with the Rallidae; the penguin was for a long time considered to belong to the Alcidae; grebes and loons are closely related even though in different orders; and of course ibises resemble curlews externally. No claim is made that the birds in either of the two groups of large, anomalous birds have much in common—"the biggest of this kind, having each something singular, and being not reducible to any other tribe, which therefore as straglers and anomalous birds we have placed by themselves, though they agree in nothing but their bigness" (Willughby, 1678: p. 273).

There is a source of confusion in that there are *three* main divisions of water birds in the text itself. "The third book is tripartite: the first part takes in all Birds that *wade* in the waters, or frequent watery places, but swim not; the

[1] The table of water birds proposed by Willughby and Ray has been incorrectly reported by both Raven (1942) and Allen (1951).

TABLE I—A TABLE OF WATER-FOWL

AA . . . such as frequent waters and watery places, to seek their food, and are all cloven-footed. These are either
- I. the greatest of this kind, anomalous birds, as the crane, jabiru, etc. [Gruidae, Ciconiidae, Cariamidae, Anhimidae]
- II. the lesser, which are either
  - *A. piscivorous, that feed upon fish, as the heron, spoon-bill, stork, etc. [Ardeidae, Threskiornithidae, Ciconiidae]
  - *B. mudsuckers and insectivorous with
    1. very long bills, whether
       a. crooked, as the curlew, whimbrel, etc. [Scolopacidae, †Threskiornithidae]
       b. streight, as the woodcock, godwit, etc. [Scolopacidae, †Aramidae]
    2. middle-sized bills, as the sea-pie, redshank, etc. [Recurvirostridae, Haematopodidae, Scolopacidae, Burhinidae]
    3. short bills, as the lapwing and plover [Charadriidae]

B . . . such as swim in the water; these are either
- *I. cloven-footed, as morehens, coot, etc. [Rallidae, †Jacanidae]
- II. whole-footed, either
  - A. long-leg'd; anomalous birds, the flammant, the avosetta and corrira [Phoenicopteridae, Recurvirostridae]
  - B. short-leg'd, having
    - *1. but three toes in each foot, the penguin, the razor-bill, etc. [†Spheniscidae, Alcidae]
    - 2. four toes in each foot, either
      - *a. all connected together by intervening membranes, the pelecan, the soland goose, etc. [Pelecanidae, Sulidae, Phalacrocoracidae, Phaëthontidae, Anhingidae]
      - b. the back-toe loose; and these are either
        - i. narrow-bill'd, the bill either
          - aa. blunt and hooked at the tip, either
            - *j. serrate, divers [Anatidae]
            - *jj. not toothed, the puffin [*i.e.*, Manx Shearwater], etc. [Procellariidae]
          - bb. sharp-pointed and streighter . . .
            - *j. short-winged and divers, called douckers [† Colymbidae, † Gaviidae]
            - *jj. long-winged and much upon the wing, called gulls [Laridae, Stercorariidae, Phalaropodidae]
        - *ii. broad-bill'd, which may be divided into the
          - aa. goose-kind, which are the bigger [Anatidae]
          - bb. duck-kind, the lesser, which are either
            - j. sea-ducks, that dive much [Anatidae]
            - jj. river and plash [*i.e.*,marshy pools] ducks [Anatidae]

second, such as are of a *middle* nature between swimmers and waders, or rather that partake of both kinds, some whereof are cloven-footed, and yet swim; others whole-footed, but yet very long-leg'd like the waders: the third is of whole-footed, or fin-toed Birds, that *swim* in the water" (Willughby, 1678: Preface). The whole-footed, long-leg'd corrira, which Ray took from Aldrovandi, is aparently a fictitious bird.

These are the beginnings of ornithological classification—a chain of men and ideas stretching over more than two thousand years. The groundwork had been laid, and the stage was set for Linnaeus and the opening of the modern period.

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Summary

The first scientific classification of birds appeared in 1676 in Willughby and Ray's *Ornitholofiae.* But Aristotle was the first

to suggest dividing birds into groups. He also contributed several ideas to the subject of classification. The line next goes to Pliny, the only other ancient to suggest a classification, and then skips to the Renaissance. William Turner in 1544 listed birds under a number of Aristotle's descriptive terms. Conrad Gesner and Pierre Belon both published important books in 1555, to be followed almost fifty years later by Ulisse Aldrovandi. The scheme of Walter Charleton appeared in 1668, immediately preceding Willughby and Ray's famous classification. Various details and quotations from original sources are presented.

LITERATURE CITED

ALDROVANDI, ULISSE. 1599–1603. . . . Ornithologiae, hoc est de avibus historiae. 3 vols. Bononiae.

ALLEN, ELSA G. 1951. The history of American ornithology before Audubon. *Trans. Amer. Philos. Soc.*, (New series), *41*, Part 3.

ARISTOTLE. 1910. Historia animalium. Translated into English by D'Arcy Wentworth Thompson. Oxford University Press, Oxford.

BELON, PIERRE. 1555. L'histoire de la nature des oyseaux. Paris.

CHARLETON, WALTER. 1668. Onomasticon zoicon. London.

CUVIER, GEORGES and AUBERT DUPETIT THOUARS. Notice of Ray (from the Biographie universelle). In Lankester, Edwin. 1846. Memorials of John Ray, pp. 95–108. Printed for the Ray Society, London.

EVANS, A. H., Ed. 1903. Turner on birds: a short and succinct history of the principal birds noticed by Pliny and Aristotle. Cambridge University Press, Cambridge.

GESNER, CONRAD. 1555. . . . Historiae animalium liber III. qui est de avium natura. Tiguri.

LONES, THOMAS E. 1912. Aristotle's researches in natural sicence. West, Newman & Co., London.

NEWTON, ALFRED. 1896. A dictionary of birds. Adam and Charles Black, London.

PLINIUS SECUNDUS, C. 1635. The historie of the world: commonly called, the Natural historie of C. Plinius Secundus. Translated into English by Philemon Holland. London.

RAVEN, CHARLES E. 1942. John Ray, Naturalist; his life and works. Cambridge University Press, Cambridge.

RAY, JOHN. 1686–1704. Historia plantarum. 3 vols. London.

SINGER, CHARLES. 1931. The story of living things. Harper & Brothers, New York.

STRESEMANN, ERWIN. 1951. Die Entwicklung der Ornithologie. F. W. Peters, Berlin.

WETMORE, ALEXANDER. 1951. A revised classification for the birds of the world. *Smiths. Misc. Coll., 117*, No. 4.

WILLUGHBY, FRANCIS. 1676. . . . Ornithologiae. . . . London.

——— 1678. The ornithology of Francis Willughby. . . . Translated into English, and enlarged . . . by John Ray. London.

ZIMMER, JOHN TODD. 1926. Catalogue of the Edward E. Ayer ornithological library. Field Museum Press, Chicago.

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Major Evolutionary Lines in Water Mites

RODGER MITCHELL

OVER the years many data have accumulated on life histories and the larval forms of water-mites. This information, when collated, indicates a broad uniformity in the water-mites and, moreover, points up phyletic lines that have not been well established on other data. These broad phyletic lines above the family level are of utmost significance in classification. When the data reviewed here are greatly supplemented it will be possible to refine critically the classification. At present only the potential value of certain data can be pointed out. It is true that the differentiation and definition of species is still the most pressing task in acarine taxonomy, but it must be emphasized that the refinement of higher classification in this group will depend on an accurate understanding of the major phyletic lines considered below.

Those unacquainted with the water-mites are immediately overwhelmed by the marked differences in adult morphology of the more than forty families. Students of the group seem to learn the families as entities. There are recognizable groups of related families but as a general rule the families appear unique. Adult exoskeletal features give, at best, an inadequate picture of relationships above the family level. Adult structure need not be reviewed here; only a brief outline of the kinds of characters that assume particular importance in classification is relevant to the main discussion.

Sclerites of the adult are used in the discrimination of species and the definition of families, and four main groups of structures are particularly significant: genital structures, body sclerites, mouthparts, and the legs and coxae. Both mouthparts and leg structures are conservative. Certain divergent families have peculiar mouthparts, but as a rule the trends seen in the structure of legs and mouthparts are difficult to categorize and of little value in family definitions. External genital structures and body sclerites are the main features considered in the separation of water-mite families.

The striking discontinuities and the resultant uncertainty about relationships are better explained through an understanding of the manner in which the features of the exoskeleton may develop. Sclerites were formed as arthropods evolved from a soft-bodied form. Obviously, all arthropods acquired an exoskeleton at one time, but the order Acarina is exceptional in that only a few, small sclerites of the legs are homologous throughout the order, and the differences in other exoskeletal features are so great as to suggest that they evolved recently. In addition, the sclerites of mites are often the result of the appearance of entirely new sclerites and not just modifications of existing sclerites, as is the usual case in other arthropod orders.

The development of body sclerites was a recent occurrence in water-mite evolution. Many families have a unique set of independently evolved body sclerites, and these sclerites commonly serve as insertions for the enlarged muscles needed for swimming. The presumed ancestral form, as well as certain extant primitive water-mites, are without body sclerites. These animals possess a weak musculature and have no sclerotizations of the body wall. They are very close to terrestrial mites, and are poor swimmers. Terrestrial locomotion, or, more precisely, movement through the medium of air, requires less power than movement through water; hence, the heavier musculature and stronger supportive structures found in

all major groups of water-mites seem closely related to more efficient locomotion in water.

Phylogenies based on sclerites alone indicate that there was a soft-bodied ancestor which gave rise to a large number of unrelated lines, each of which may have a unique set of sclerites. This is a much-abbreviated picture of water-mite evolution. A great many sets of body sclerites have been described, but before homologies between body sclerites can be understood, musculature as well as the exoskeleton must be carefully studied. At present, there would appear to be no less than twenty-five independently evolved sets of body sclerites in the group. Phylogenies based on data reviewed below indicate evolutionary lines much broader than those shown by adult features. Considerable evolution of larval and behavioral features must have occurred before the adult acquired body sclerites, and the broader phyletic lines, marked by larval and behavioral features, are reviewed below with the suggestion that they deserve a more prominent place in systematic studies.

Life Histories

The first observations on water-mites recorded specimens attached to insects. These were larvae. Since then much has been learned from the rearing of larvae attached to field-collected hosts. Complete life histories have been followed in the laboratories of Münchberg, Uchida, Imamura, and Mashuda. From time to time other studies have appeared but the workers named are among the most active. These data have contributed toward understanding life histories of many common Holarctic families. Some of these are listed in Viets (1936) but many papers not pertinent to Viets' study have never been reviewed. While a critical review is not appropriate to this paper, key references will be cited insofar as possible. Under each heading examples have been taken from personal observations and references to important papers are appended. My observations are usually verifications of previous work.

By definition, the water-mites are an ecological assemblage and this category is without phylogenetic significance (Mitchell, 1954*b*). However, all lines of water-mites appear to have been derived from some terrestrial trombidiid and, as a result, the basic life history of all water-mites is the same. The life history includes three active stages: the six-legged larva; the eight-legged, sexually undeveloped nymph; and the adult. Each of these stages is preceded by a developmental or quiescent stage: the egg, the nymphochrysalis, and the teliochrysalis, respectively. Usually only the active stages are considered in this study.

The various life-history types, each diagrammed and numbered in Figure 1, will be considered in levels. The levels represent a change in the general nature of one or two of the active stages from that of the preceding level and are designated by Roman numerals.

Level I. This is the life history common to all major groups of water-mites. Nymphs and adults are free-living predators. The larvae are active and when they locate a host they attach themselves and feed on the host while attached to that one spot. Not only does the larva receive nourishment from the host but it is passively transported as well. This is an important factor in the dispersal of the species. The life-history pattern was established as being widespread by Wesenberg-Lund (1918) and later supported by the studies of Lundblad (1927), Münchberg (1935, 1954) and the Japanese investigators (mostly listed by Imamura, 1954). Level I life history is thought to typify the primitive members of virtually all families.

Level II. Two different life histories are derived from the first level: one by extension of the larval association with the host (type II*a*), the other by elimination of larval parasitism (type II*b*).

The parasitic association with the host is extended in the Eylaidae and Hydrachnidae as indicated in life-history type II*a*. Once attached to the host the larva remains attached until the nymph is fully

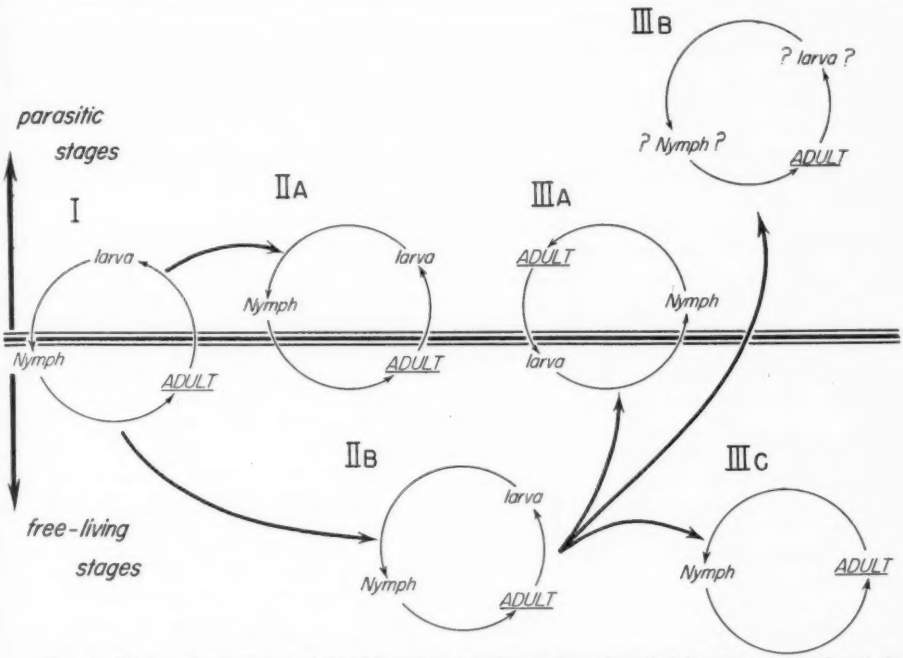

FIG. 1. The various types of life histories are shown here in what is supposed to be their phylogenetic relationship. A circle represents each life cycle; all active stages are indicated and the circle placed so that the free-living stages lie *below* the heavy horizontal line and parasitic stages lie *above* the line. Roman numerals designate levels or evolutionary steps, and individual types are distinguished by the addition of a letter.

formed. It then emerges from the larval skin. Within a few days the nymph transforms to the adult. The extent of the association between nymph and host is unknown, but the extraordinary larval engorgement may substitute for some of the feeding usually done as a nymph. Nymphal development is carried on while the organism is attached to the host but there is also the usual free-living nymphal stage. This extension of larval association up through the nymphal development cannot be clearly indicated in Figure 1.

Feeding habits are varied. Eylaid nymphs and adults feed on ostracods, but in the Hydrachnidae there is some question as to the food. The tendency of *Hydrachna* to attach themselves to plants, and the peculiar structure of the mouthparts lead some investigators to suspect them of being herbivorous.

Excellent life-history studies have been published for *Hydrachna* (Mashuda, 1934; Stout, 1953*b*) and for *Eylais* (Stout, 1953*a*). As discussed later, larval morphology proves that the Eylaidae and Hydrachnidae are unrelated; hence, type II*a* life history must have evolved separately in the two lines. It is interesting to note that these unrelated families, which have independently acquired the same peculiar life history, should contain species of very similar ecology. The factors involved in this ecological parallelism are well worth study.

Larval parasitism is eliminated in life history type II*b*. Larvae may feed but feeding has not yet been observed.

Level III. All three life histories assigned to this level are derivatives from type II*b* in which the larva is nonparasitic. These forms are either secondarily parasitic (types III*a* and III*b*) or else

have suppressed the active larval stage. Parasitism was developed secondarily in two different ways. *Astacacroton*, an Australian genus that parasitizes crabs, probably belongs here but knowledge of its habits is so meagre that even a provisional placement is impossible.

The life history designated type III*a* is that of the genera *Unionicola* and *Najadicola* (family Unionicolidae). The evolution of these groups has received detailed treatment elsewhere (Mitchell, 1955). The larvae are never parasitic, probably never feed, and are, through their swimming, the main means of dispersal of the species. Adults and nymphs have secondarily acquired a parasitic habit which differs from the parasitic habit of all other water-mites in two ways: the hosts are molluscs or sponges, never arthropods, and secondly they are ectoparasites that feed at frequent intervals rather than engorge themselves at one spot.

Type III*b* is represented by *Parasitalbia sumatrensis* Viets. The adult female of this mite was found engorged and attached to an ephemerid (Viets, 1935). No more is known. Absence of the larval and nymphal skins at the site of engorgement would indicate that the adult parasitism is not an extension of larval parasitism such as was developed in type II*a*. This tentative assignment is also influenced by the fact that many other mites in this family probably have non-parasitic larvae.

There is no active larval stage in type III*c* life history. This is a continuation of the trend established in type II*b*. The larval stage, which did little, if any, feeding, and was ineffectual in dispersal, has been suppressed in this type of life history. Larval differentiation occurs within the egg and following that there is the immediate development of the nymph, the active stage that leaves the egg.

Lundblad (1927) and Stout (1953*b*) established this life history for *Piona*. The life history, which is common to many still-water forms and is probably typical of most rheophilic species, has developed independently many times. The difficulty of rearing stream forms in the laboratory limits the studies on such forms. However, the eggs of many rheophilic species of Sperchonidae, Axonopsidae, and Torrenticolidae are extremely large and few in number. This is considered presumptive evidence that the young emerge at an advanced stage of development, the nymph.

Larval Structure and Behavior

The more conspicuous behavioral traits are those shown by the larva when it is actively moving about prior to parasitizing a host. These traits may be separated into those that orient the animal in locating and parasitizing the host, and those expressed in locomotor behavior. No experimental data on larval behavior have yet been recorded but the many field and laboratory observations provide data adequate for this discussion.

As the mite moves about, it orients to general features such as illumination, gravity, and temperature. These responses doubtless tend to increase the probability that the larva will contact a suitable host. Usually the larva stops when the host is reached. If the mite is one that attacks mature hosts, it will move over the body of the host and shortly attach itself for feeding. Other larvae are attracted by the pupa or terminal nymph of the host. In such cases the larva comes to rest on the host, either randomly or at a specific location, depending on the mite species. In either case there is no feeding. It is only when the host imago emerges that the larva becomes active. It then crawls onto the newly emerged host and attaches itself for feeding. All water-mite larvae feed at one spot, and when fully engorged they drop off the host. The only exceptions to this are those water-mites with a type II*a* life history.

The most obvious larval features are locomotor adaptations. There are two types of locomotion among larvae. In one case the larvae walk about on the water surface. Because this involves movement through the medium of air they must be called aerial larvae. The other group is

aquatic and consists of forms that are active swimmers. That neither group is a natural assemblage is shown by the structure of the mouthparts and the parasitic behavior of the larvae. Each locomotor type includes two divergent lines. Since the general form associated with each type of locomotion is superficially similar, it will be most convienient to discuss the shared adaptive convergences of each locomotor type. Then phylogenetically significant features can be contrasted in the definition of the larval groups.

Walter (1922) made the first major contributions to an understanding of larval relationships. Later Lundblad discussed some aspects of larval relationships (1927) and Viets (1936) published a descriptive key to the larvae of German water-mites. All the data considered below are well-known facts, and the larval groups that are used here have been named (Walter, 1922; Bader, 1955), but these authors did not fully consider the relationships and biology of the categories.

Aerial Larvae (Fig. 2*a–d*). There is no reason to believe that these larvae were ever aquatic in habit. Adults of all the groups involved are primitive, soft-bodied, and rather inefficient in swimming. Evidently the adults and nymphs evolved aquatic adaptations but the larvae remained terrestrial, except for the fact that they walk on the water surface rather than the ground. The features of terrestrial larvae are a spherical membranous body with relatively weak apodemes and few, if any, sclerites, and very long setae with modified bases which are probably receptors of vibrations. The characteristic facies of such larvae is the result of their having a spherical body thickly covered with setae.

Propulsion over the water surface is an easy matter for any animal under a third of a millimeter in length. Leg muscles need to do little more than support the body. Thus the coxae, which provide insertions for the extrinsic leg muscles, are small and lightly sclerotized. Sometimes the coxae are differentiated from the adjacent membrane only by differences in surface texture and only the marginal apodemes are sclerotized. Weak sclerites indicate weak leg musculature. The coxae are also small and do not extend far toward the mid-line of the body, indicating that the leg muscles are short as well as weak.

Long axes of the coxae point to a single mid-ventral point. This results in the first legs extending anteriorly, the middle legs laterally, and the hind legs posteriorly. Movement of the entire leg relative to the body may be different for each leg since only the movement of the end of the leg on the substrate is important in aerial locomotion.

There are no data on the inherent properties of sensory setae in mites, but certain general principles may apply. The vibration receptors of terrestrial mites must be delicate, a fact that might be expected to show up in their proportions and insertion. Chemoreceptors must be concentrated on tips of appendages that contact moist surfaces or else have a special moisture-conserving surface. These principles seem to apply to the sense organs of aerial larvae. The elongated body setae that must be touch and vibration receptors have a membranous basal ring which is usually surrounded by a sclerotized plate. Such setal bases are characteristic of these aerial larvae but not of aquatic larvae. Tips of the appendages are provided with membranous lobes and a variety of fine walled setae closely resembling certain chemoreceptors of other arthropods. There are no other special structures of the body surface that might be considered chemoreceptors.

The general facies of the different aerial larvae are similar because of convergent adaptations to aerial locomotion. Variation in the degree of specialization may occur as exemplified by the very weak coxae of hydrovolziids and the very large setae of thyasids, but the rotund body with non-parallel leg axes and the long, abundant body setae characterize all aerial larvae.

There are two phyletic lines within this group, and these two lines are distinguished from each other by details of the setal arrangement and the mouthparts. The behavior in parasitism is also quite different in each line.

Hydrovolziid Larvae (Fig. 2*a–b*). These divergent forms all belong to a single family of uncertain position, the Hydrovolziidae. Both larval and adult structure is peculiar, and relationships of the group are obscure. Resemblances between Hydrovolziidae and the marine Halacaridae seem to be superficial parallelisms. Larvae of the genus *Hydrovolzia* have been described (Walter, 1922; Lundblad, 1930) and one life history has been recorded (Mitchell, 1954*a*).

The setae of the dorsum are peculiarly arranged and the small anteriorly-placed dorsal shield is unique. No other water-mite larvae have club-shaped setae. Though most of the setae are rather long, there are no sclerites associated with their bases. Possibly the mouthparts are derived from the basic water-mite structure but they are so modified that this might be questioned at present. The supportive sclerite of the mouthparts is extremely broad and short. Location and movement of both oral appendages are radically different from those of any other water-mite larvae. Chelicerae lie in a nearly dorsoventral plane on the anterior surface. The palps are located laterally and move in a meso-anterior plane when flexed.

The behavior of the active larvae is rather simple. They are slow moving. When a host is contacted the larvae immediately climb up the appendages and attach themselves to the host's body. *Hydrovolzia gerhardi* Mitch. attacks the active terminal nymphs or adults of a mesoveliid bug (Mitchell, 1954*a*). Once attached the larva remains at one spot and engorges. Distention of the body occurs between the second and third coxae and posterior to the third coxae.

Thyasid Larvae (Fig. 2*c–d*) resemble the terrestrial Trombiculidae and Trombidiidae. In fact the larva of one water-mite genus (*Limnochares*) was assigned to the family Trombiculidae and described as *Hemitrombicula* Ewing. All these larvae seem to be obviously derived from a trombidiid-like ancestor. A link between the two groups is seen in *Stygothrombium* (Viets, 1932) which has many structural features of a trombidiid but its aquatic habits resemble those of a water-mite, members of the family Protziidae in particular. Indeed, the separation of water-mites, the Trombidiidae, and the Trombiculidae by major structural features is difficult.

All members of this group possess a complex group of dorsal sensory setae that may be associated with a median dorsal sclerite. This group of structures, termed the frontal organ, is closely related to similar structures of other Trombidiformes. Setae of the dorsum are always long and usually the leg chaetotaxy is also well developed. Fusion of segments 2 and 3 may reduce the normally six-segmented leg to a five-segmented leg but usually does not reduce the length of the leg.

Mouthparts are unmodified from the typical trombidiid pattern. Chelicerae lie on the dorsal surface of the capitulum and move longitudinally. The palps, which rest in sockets near the base and extend anteriorly, function as grasping organs.

Thyasid larvae move about on the surface of the water. With one exception they parasitize the aerial adults of some aquatic insect. The exception, the larva of the genus *Eylais*, attacks corixid bugs or haliplid beetles. Those larvae invade the plastron of air under the host's forewings when the host is at the water surface. The larva remains in this pocket of air throughout its feeding. Therefore even though these larvae attack an aquatic animal they never pass through the surface film and, in reality, never leave the aerial habitat.

Most members of this group are dipteran parasites. The larvae locate the host pupa and cluster about the breathing horns of the pupa. When the imago emerges the larvae climb onto the host and dig in their mouthparts before the

cuticle is fully hardened. Engorgement follows and the distention of the body occurs both anteriorly and posteriorly to coxae III.

Knowledge of the Holarctic groups indicates that the superfamilies Limnocharae and Hydryphantae have larvae of this type. There are several Southern Hemisphere families about which nothing is known. The families for which there is positive information concerning the larvae are the Proziidae. Hydryphantidae, Eylaidae, Piersigiidae, and Limnocharidae.

Aquatic Larvae (Fig. 3*a–d*). These larvae are greatly modified from the ancestral form. Most features of these larvae are direct adaptations for movement through a dense medium, water. The shape of the larvae reduces the resistance to movement through water and the locomotor apparatus is modified to increase the power and modify the direction of the stroke of the legs. All aquatic larvae are flattened dorso-ventrally. Both the dorsal and the ventral surfaces tend to be covered by a sclerotized shield. Most setae are modified or lost. The large setae that remain project parallel to the long axis of the body, and therefore do not interfere with streamlining.

Any increase in the power of leg action is necessarily limited and determined by the articulation of the leg to the body, and the musculature of the legs. All muscles activating the second to sixth segments of the legs are flexors. Extension is effected by the pressure of fluids within the body. Hydrostatic pressure would seem to be difficult to control precisely and the power formed in this way is limited by the strength of the body wall. Muscular power may be increased as long as there is room for muscles and it is, moreover, under precise control. Therefore it seems logical that power should be developed in flexion and this is the case in water-mites. Leg adduction is the power stroke.

The legs of water-mites, like those of most Acarina, tend to have the basal segment of the leg articulated in such a way that its plane of movement is vertical. This means that if the legs are to propel the body forward, the power stroke must begin with the legs extended anteriorly. The legs are adducted and this imparts a forward motion to the body. This is actually a theoretical ideal that appears to outline a trend that is particularly useful in explaining certain features of the legs and coxae of water-mite larvae.

Leg and coxal structure of aquatic larvae seem to follow the trend just outlined. The legs tend to extend anteriorly, and the coxae, which support the muscles activating the basal leg segment, tend to extend posteriorly from the articulation. This is most pronounced in the hygrobatid type (Fig. 3*d*) but it is also apparent in the hydrachnid type (Fig. 3*b*) especially in comparison with aerial forms. The coxae and apodemes of these forms are heavily sclerotized and well developed. The strengthening of sclerites that serve as muscle attachments is closely correlated with greater efficiency in swimming.

The reduced chaetotaxy of all aquatic forms reduces resistance of the body to movement through water and eliminates the special modifications of sensory structures that were essential for terrestrial animals. As is common in other aquatic animals, the chemoreceptors may be widely distributed over the body. There is no known structure of aquatic larvae that might be a local concentration of modified chemoreceptors.

All obvious features of aquatic larvae are purely utilitarian. The flattened body, the strengthened sclerites, and the anterior position of the legs aid in effective swimming. All elongate setae project parallel to the long axis of the body and no modified chemoreceptors are recognizable. All these features contribute directly to an increased locomotor efficiency.

The two phyletic lines have aquatic larvae that differ in the degree of specialization. The hydrachnid type is relatively unspecialized and seems to represent an entirely independent line of evolution. It is the only primitive family of water-

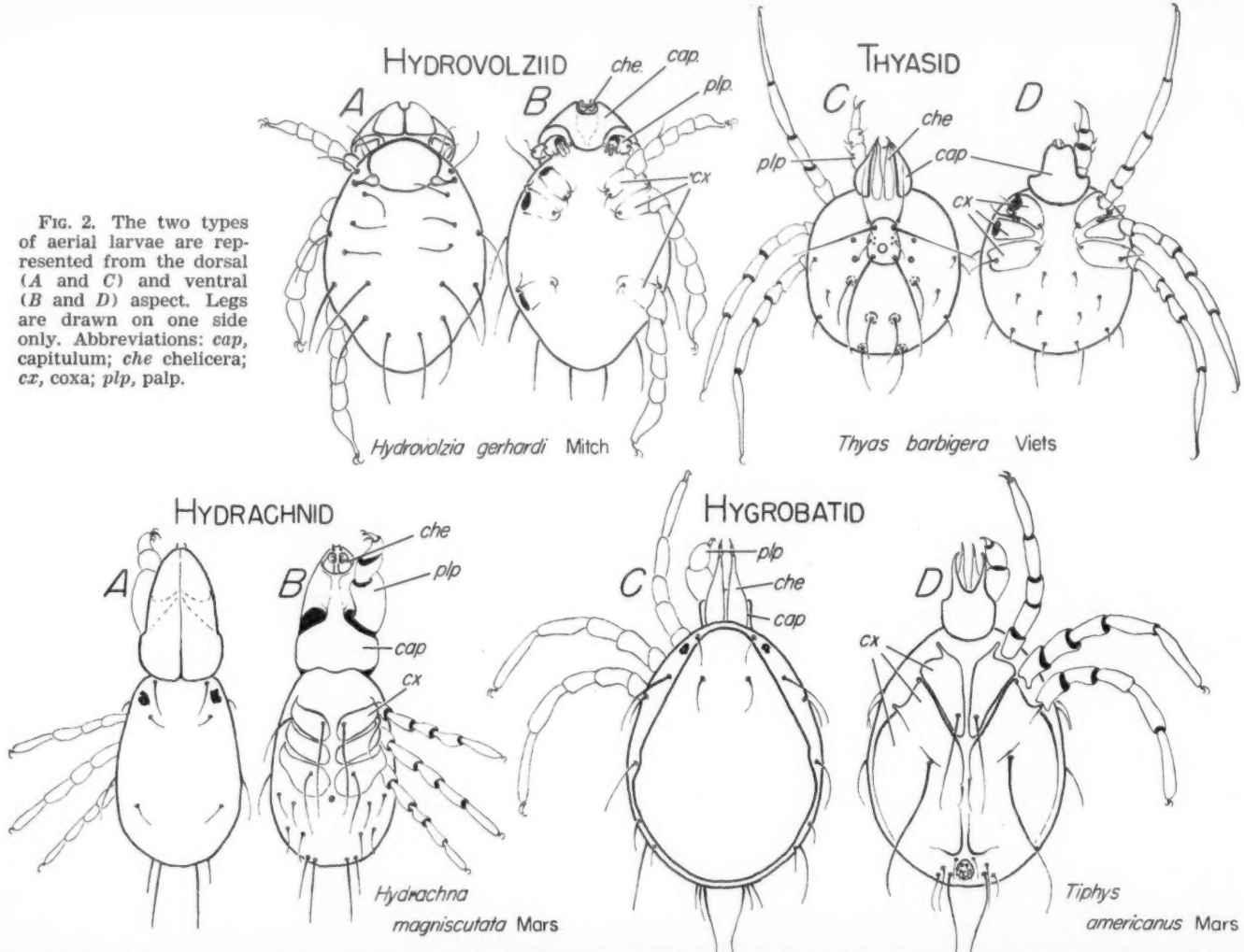

FIG. 2. The two types of aerial larvae are represented from the dorsal (*A* and *C*) and ventral (*B* and *D*) aspect. Legs are drawn on one side only. Abbreviations: *cap*, capitulum; *che* chelicera; *cx*, coxa; *plp*, palp.

FIG. 3. The two types of aquatic larvae are represented from the dorsal (*A* and *C*) and ventral (*B* and *D*) aspect. Legs are drawn

mites in which the larvae are aquatic. Larvae of the hygrobatid type are highly modified swimmers that seem to have evolved from the thyasid type. These two larval types differ in locomotor adaptations but they are similar in their parasitic habits.

Hydrachnid Larvae (Fig. 3*a–b*). The small family Hydrachnidae which has this type of larva may well be independent of other water-mites. As mentioned, the modifications of the leg bases are not extreme in this form but the relative positions of the third and fourth coxae are important, though not highly developed, modifications contributing to more effective swimming.

The most distinctive features of hydrachnid larvae are the huge mouthparts. They are nearly as large as the rest of the body. In swimming, these mouthparts are pressed against the venter but when feeding they are extended. The main body of the capitulum is broad and quite elongate. Its dorsal surface is covered by a thin sclerite. The broad, but small, chelicerae are located ventrally in a circular cavity near the tip of the capitulum. Palps are inserted in a deep depression about mid-way along the capitulum. When flexed their predominant movement is in a mesal direction. Only the results of sound anatomical studies will indicate the significance of similarities in certain external features of hydrovolziid and hydrachnid mouthparts.

A dorsal shield covers the whole dorsum in the unengorged larva. Three pairs of setae arise on the shield and two pairs around its edge. All these are short setae with unmodified bases. The chaetotaxy of the venter is more developed. Prominent setae arise on the first and third coxae. A heavy seta lies just lateral and posterior to the first coxa, and three rows of small setae lie posterior to the third coxae. There are four fine setae in each row.

Swimming of these larvae is not powerful; however, it keeps them in the upper levels of the water. There they contact a host animal, usually a hemipteran nymph or imago, or a beetle imago. The host is always in an active stage and larval attachment can be almost anywhere on the host's body. Any restrictions of the site of parasitism seem to be determined by the ability of the host to dislodge the parasite. In a few instances the larvae may be specific in their site of attachment. Following attachment the larvae engorge. Distention of the body occurs posterior to the third coxae. Peculiarities of the life history of these larvae have been fully discussed above (life-history type II*a*).

Hygrobatid Larvae (Fig. 3*c–d*). The great majority of the water-mites, the superfamilies Pioninae, Axonopsae, Mideopsae, and Arrenurae, are included here. In addition the families Sperchonidae and Lebertiidae of the Lebertiae belong here. Placement of the other families of this superfamily must await knowledge of larval forms, for the transitional nature of the larvae of *Sperchon* indicates that some aerial larvae might be found in the Lebertiae.

All these larvae are strictly aquatic and most of their obvious structural features may be interpreted as straightforward adaptations to swimming. The dorso-ventrally flattened body is enclosed by very large dorsal and ventral plates. There are, at the most, three or four small simple setae anteriorly-placed on the dorsal shield. Several other small setae may be located along the margin of the dorsal shield. The one or two pairs of long setae which originate at the posterior extremity of the body always extend parallel to the long axis of the body. Setae of the venter are variable and the coxae usually bear one or two elongate setae. A few small setae are associated with the so-called anus.

The expanded coxae which cover the venter and the muscle scars indicate that these sclerites provide origins for the elongate muscles activating the basal segments of the legs. In addition, the legs are shifted to an anterior position. Hence,

Fig. 3. The two types of aquatic larvae are represented from the dorsal (*A* and *C*) and ventral (*B* and *D*) aspect. Legs are drawn

the long axis of each coxa tends to be in an antero-posterior orientation. This extreme in the development of swimming modifications as discussed above is characteristic of hygrobatid larvae. Legs of these larvae are proportionally shorter than are those of larvae of aerial mites. They have legs with five segments rather than the more usual number, six.

There is no conspicuous difference between the mouthparts of these larvae and those of thyasid larvae. All differences within the group are variations in the relative size and shape of the various elements. Reduction or loss of a palpal segment may occur.

These larvae can swim swiftly through the water. The path they follow appears to be erratic and undirected. If a pupa or terminal nymph of the appropriate host is encountered, the larvae come to rest on the animal. The larvae do not seem to be directed to, or attracted by, the host from any great distance. When the imago emerges the larvae again become active and crawl onto the host and attach themselves, often at a specific location. Engorgement follows and distention of the integument occurs posteriorly and lateroposteriorly to the third coxae.

Lundblad (1927) notes the intermediate combination of characters in *Sperchon*, and with certain reservations assigns *Sperchon* to the advanced larval type. Since that practice is followed here, the basis for the decision should be outlined. *Sperchon* has enlarged coxae; although they are not so large as those of other hygrobatids, they do approach them in size. The setae of *Sperchon* are also much reduced. Though the larvae lack extreme structural specializations for aquatic life, they are strictly aquatic in habits. Structurally *Sperchon* lies between the thyasids and hygrobatids but in habits it is a hygrobatid. Existence of this form supports the contention that hygrobatid larvae evolved from thyasids. Unfortunately the assignment of *Sperchon* to one group may obscure its significance as an intermediate form.

Discussion

The data just discussed are diagrammed in Figure 4. The features that distinguish the four larval types have been

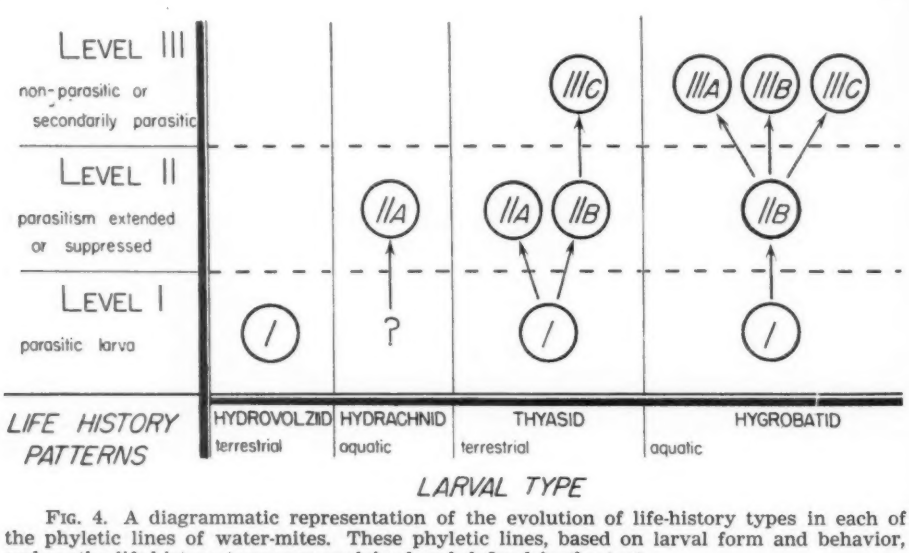

FIG. 4. A diagrammatic representation of the evolution of life-history types in each of the phyletic lines of water-mites. These phyletic lines, based on larval form and behavior, and on the life-history types are explained and defined in the text.

considered and there remains the task of pointing out how the evolution of life histories (Figure 1) fits in with the categories based on larval behavior and structure.

With one exception, the hydrachnids, the basic life history is common to all groups, and the evolution of life histories in each group may be correlated with a number of other features. One family of the thyasid group, the Eylaidae, has a type II*a* life history and these are the only thyasid larvae that parasitize long-lived imagos of aquatic insects, i.e., beetles and hemipterans. It seems unlikely that parasites of aquatic dipteran imagos could extend the time of association with the host for the life span of the imago is brief. Most thyasids parasitize dipteran imagos. The commonest modifications in thyasid life histories involve suppression of the parasitic habit (life history types II*b* and III*c*).

In all known life histories of hygrobatids the host is the aerial imago of some aquatic insect and an extended association with the host may not be possible because of the brevity of the host's active life. Thus larval parasitism is commonly suppressed in hygrobatids but in three or four instances parasitism was acquired secondarily.

In addition to the diversity of highly modified third level life histories the hygrobatids are also the most diverse in adult structure. They have become successfully established in a greater variety of habitats than has any other group. Hygrobatid larvae are wholly aquatic. Thus, they can live in turbulent waters where the larvae can swim in the rather quiet water film over the bottom or through gravel. The surface of such waters is unsuited for aerial larvae. Hygrobatids may invade deep waters for their entire life history may be passed without access to the surface. Forms of other groups must live on the water surface at one stage (hydrovolziids or thyasids) or else they attack hosts that must reach the water surface to breathe (hydrachnids). This limits these forms to shallow, still bodies of water or the quiet zones of lakes. Thus the hygrobatids, the only group in which the larvae are not limited to shallow, still waters, exhibits the greatest diversity in form and ecology.

Conclusions

These behavioral, structural, and life-history features all fit together to show the existence of broad, interrelated groups. Further study of these features appears likely to provide sound support for the existence of a few broad phyletic lines in water-mites rather than many independently evolved small families. Thus it appears that the kinds of data used with success in differentiating species may not be equally useful in the definition of higher categories.

LITERATURE CITED

BADER, C. 1954. Das Darmsystem der Hydracarinen. *Rev. Suisse Zool., 61*:505–549.

IMAMURA, T. 1954. Studies on water-mites from Hokkaido. *Journ. Hokkaido Gakugei Univ.*, Sect. B, Suppl. No. 1, pp. 1–148.

LUNDBLAD, O. 1927. Die Hydracarinen Schwedens I. *Zool. Bid. Uppsala, 11*:185–540.

——— 1930. Hydracarina. *Zoology of the Faroes, 48*:1–65.

MASHUDA, Y. 1934. Notes on the life history of *Hydrachna* (*Schizohydrachna*) *nova* Marshall. *Journ. Sci. Hiroshima Univ.*, Ser. B, Div. 1, *3*:33–43.

MITCHELL, R. D. 1954*a*. A description of the mite *Hydrovolzia gerhardi* new species, with observations on the life history and ecology. *Chicago Acad. Sci., Nat. Hist. Misc.*, No. 134, 9 pp.

——— 1954*b*. Check list of North American water-mites. *Fieldiana: Zoology, 35*:29–70.

——— 1955. Anatomy, life history and evolution of the mites parasitizing mussels. *Misc. Pub. Univ. Mich. Mus. Zool.*, No. 87, 27 pp.

MÜNCHBERG, P. 1935. Zur Kenntniss der Odanatenparasiten, mit ganz besonderer Berüchsichtigung der Okologie der in Europa an Libellen schmarotzenden Wassermilbenlarvae. *Arch. Hydrobiol., 29*:1–120.

——— 1954. Zur Kenntnis der an Culiciden schmarotzenden *Arrenurus*-Larven. *Zeitsch. f. Parasitenkunde, 16*:298–312.

STOUT, V. 1953*a*. *Eylais waikawae* n. sp. (Hydracarina) and some features of its life history and anatomy. *Trans. Roy. Soc. New Zealand, 81*:389–416.

——— 1953*b*. New Species of Hydracarina, with a description of two. *Trans. Roy. Soc. New Zealand, 81*:417–466.

VIETS, K. 1932. Weitere Milben aus unterirdischen Gewässern *Zool. Anz., 100*:173–176.

——— 1935. Die Wassermilben von Sumatra, Java, und Bali nach den Ergebnissen der Deutschen Limnologischen Sunda-Expedition. *Arch. Hydrobiol.,* Suppl. Bd. *13*:595–738.

——— 1936. Die Tierwelt Deutschlands und der angrenzenden Meeresteile. Wassermilben oder Hydracarinen. Teil 31–32, *7*:1–574.

WALTER, C. 1922. Die Hydracarinen der Alpengewässer. *Denkschr. d. Schweiz Naturf. Ges., 58*:60–251.

WESENBERG-LUND, C. 1918. Contributions to the knowledge of the postembryonal development of the Hydracarina. *Midd. Dansk. naturah. Foren., 70*:5–57.

RODGER MITCHELL is an Assistant Professor in the Department of Biology at the University of Florida. This paper reports some of the broader implications of detailed faunistic studies carried out at the E. S. George Reserve of the University of Michigan with the support of Grants-In-Aid from the George Reserve Scholarship Fund. This work has been greatly assisted by the cooperation and critical attention of the Curator of the Reserve, Irving J. Cantrall. A brief summary of the paper was read before the Society of Systematic Zoology at the Atlanta Meeting in December, 1956.

The Cephalocarida and Crustacean Phylogeny

(*Concluded from p. 128*)

——— 1944. On the relationships and phylogeny of fossil and recent Arachnomorpha. *Skr. Vid.-Akad. Oslo 1. M.-N. Kl.,* No. 5:1–158.

TRIEBEL, E. 1941. Zur Morphologie und Ökologie der fossilen Ostracoden. Mit Beschreibung einiger neuen Gattungen und Arten. *Senckenbergiana, 23*:294–400.

HOWARD L. SANDERS is a Research Associate at the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts. This study was made possible by a Grant-in-Aid of Research from the Sigma Xi RESA Research Fund for the summer of 1955 and by subsequent National Science Foundation support for benthic community investigations in Buzzards Bay, Massachusetts where many specimens of *Hutchinsoniella macracantha* were collected. The author would like to thank Dr. Nathan W. Riser (Woods Hole Oceanographic Institution) and Mr. Henry O. Werntz (Osborn Zoological Laboratory, Yale University) for numerous helpful suggestions. This paper is Contribution 882 from the Woods Hole Oceanographic Institution.

People and Projects

● It is with sincere regret that we record the death, subsequent to a snake bite, of Karl P. Schmidt, internationally esteemed herpetologist, who at the time of his death was Curator emeritus of Zoology at the Chicago Natural History Museum. Mr. Schmidt, a charter member of the Society of Systematic Zoology, was one of the group that helped the Society get its start.

● The XVth International Congress of Zoology will be held in London, on July 16-23, 1958. Because of the coincidence of this Congress with the Centenary of the first publication by Darwin and Wallace on evolution, several sections will be devoted to subjects having evolution as their theme. A *Prospectus and Provisional Program* can be obtained from the Registrar, XVth International Congress of Zoology, in care of The British Museum (Natural History), South Kensington, London, S.W. 7, England. Applications for membership, blanks for which accompany the prospectus, must be returned to the Registrar not later than December 31, 1957.

The Colloquium on Zoological Nomenclature of the XVth International Congress of Zoology will meet on July 9-15. Applications for this colloquium (blanks for which accompany the prospectus) must also be returned before December 31, 1957. A draft of the Rules of Nomenclature as revised at the 1948 (Paris) and 1953 (Copenhagen) Congresses will be circulated in time to permit examination at the Colloquium. The agenda for the meetings of Section 12 (Nomenclature) and those of the International Commission comprise volumes 14 and 15 of the *Bull. Zool. Nomencl.*

● The International Trust for Zoological Nomenclature has recently announced that arrangements have been made for the immediate publication in book form of the first installment of each of the "Official Lists" of valid zoological names, and of the corresponding "Official Indexes" of rejected and invalid names. Also included are the first installments of the official lists of works approved as available for zoological nomenclature, and of the official index of rejected and invalid works. The categories of names covered by these lists and indexes range from specific names to ordinal names. The total number of entries contained in the installments now to be published is about 5000.

The first of these lists, that related to generic names, was established by the Ninth International Congress of Zoology, Monaco, 1913, while the most recent were brought into existence by the XIVth congress at Copenhagen in 1953. The entries made on these lists and indexes have been promulgated from time to time by the International Commission on Zoological Nomenclature in individual "Opinions and Directions," but, owing to the large number of documents, it has become increasingly difficult for specialists to ascertain what names have so far been registered under this system. This difficulty will completely disappear on publication (now in press) of the installments, each of which will be supplied both with a full alphabetical index and also with alphabetical indexes arranged by major groups. The groups so selected will usually be classes, but, in the case of large classes containing well-recognized orders, these supplementary indexes will be on an ordinal basis.

These official lists and official indexes constitute the principal instrument devised to promote stability in zoological nomenclature and will be indispensable to all specialists engaged in taxonomic work in zoology and paleontology. Inquiries about these publications should be addressed to the International Trust for Zoological Nomenclature at its Publications Office, 41 Queen's Gate, London, S.W. 7, England.

● *The International Code of Botanical Nomenclature adopted by the Eighth International Botanical Congress, Paris, July 1954,* has been published (December 1956) by the International Bureau for Plant Taxonomy and Nomenclature of the International Association for Plant Taxonomy, Utrecht, Netherlands. Published with the financial support of IUBS-UNESCO, this work comprises Volume 8 of the *Regnum Vegetabile* (A series of handbooks for the use of plant taxonomists and plant geographers). The Code is published in English, French and German, all texts being official. In case of discrepancies between the three versions, the English text would be arbitrarily chosen as correct. A Spanish translation is also included. (A Russian translation will be published separately this year.) The Code includes "Preamble" and "Principles" (Division I), "Rules and Recommendations" (Division II) and Division III ("Provisions for modification of the Code") which consists of five appendices. The first two appendices, ("Names of hybrids and some special categories," and "Special provisions concerning fossil plants") are an integral part of the Code. Appendix III is an amended list of *nomina generica conservanda et rejicienda.* Appendices IV ("Determination of types") and V ("Guide to the citation of botanical literature"), have been retended in the Code but, as Secretary Lanjouw points out in his helpful Preface, the members of the Editorial Committee are not enthusiastic about the inclusion of these matters in the Code.

● *A Catalogue of the Works of Linnaeus,* has been issued by Sandbergs Bokhandel, in commemoration of the 250th anniversary of the birthday of Carolus Linnaeus. This catalogue which provides an annotated listing of virtually all of the writings of Linnaeus, the works of his principal pupils, and works about Linnaeus, can be obtained from The Rare Book Department, Sandbergs Bokhandel, Sibellegatan 8, Stockholm, Sweden, Price $1.00; Cr. 5: —.

● Dr. Ramadas Menon has relinquished his post in Madras and is now Systematic Entomologist, Indian Agricultural Research Institute, New Delhi-12, India.

● *Erratum:* In "X-Rays as a tool in systematic zoology" by R. R. Miller, which appeared in the March issue of SYSTEMATIC ZOOLOGY, the first line, column 2, page 30 should read: "films and use a very strong light in the" instead of, "sheets of metal and occasionally in medi-."

● The first number of the new journal *Acta Vertebratica* is devoted to a paper by Sten Larsen entitled "The Suborder Charadrii in Arctic and Boreal areas during the Teritary and Pleistocene." The journal will appear at irregular intervals and each issue will generally consist of a single paper dealing with some aspect of vertebrate zoology, chiefly ecology, ethology, zoogeography, evolution, systematics, embryology, wild-life management, or conservation. Monographic works concerning Scandinavian and northern vertebrates are especially invited, but other types of papers dealing with this subject, or works treating other faunal areas will be considered. Papers will be published in English, French or German. *Acta Vertebratica* is published by the Zoological Department of Nordiska Museet and Skansen, Stockholm, Sweden. The editors are K. Curry-Lindahl (Stockholm), B. Hanström (Lund), and B. Kullenberg (Uppsala).

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Consult recent issues for the style to be followed in the preparation of manuscripts. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.

Contributors receive galley proof but it is called to their attention that changes made in proof are expensive. The cost of alterations made in proof will be charged to the author if they exceed ten percent of the cost of composition.